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The Red Sea Mollusca described by Deshayes in Laborde's *Voyage de l'Arabie Pétrée* (1830-1834)

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ABSTRACT

The French malacologist Gérard Paul Deshayes described 13 new species of marine mollusks collected in 1828 from the northern Red Sea by two French explorers, Léon de Laborde and Louis Maurice Adolphe Linant de Bellefonds. His work was published in an expedition volume authored by Laborde. We determine the correct publication date and authorship attribution for these new species: Deshayes, in Laborde, 1833. The current systematic status of these species is discussed; seven are currently accepted as valid, five are junior synonyms, and one is a *nomen dubium*. Of the twelve known species, four are endemic to the Red Sea, four are limited to the western Indian Ocean, and four have broader Indo-Pacific distributions. This paper also discusses the publication history of the botanical chapter of this work, authored by Alire Raffeneau-Delile.

INTRODUCTION

An important but overlooked and frequently misdated expedition volume is Laborde's *Voyage de l'Arabie Pétrée*, which contains the results of an expedition in 1828 from Cairo, Egypt, to Petra, then in the Ottoman Empire and now in modern Jordan. This expedition was undertaken by two French explorers, Léon de Laborde (1807–1869) and Louis Maurice Adolphe Linant de Bellefonds (1799-1883). Laborde alone authored the expedition narrative, published in a lavishly illustrated folio volume, which also included a list of 13 new species of marine mollusks from the Red Sea illustrated on single plate and described by Gérard Paul Deshayes (1796–1875) and seven pages on the botany of that region, including several new plant species, some illustrated, described by Alire Raffeneau-Delile (1778–1850).

We demonstrate that the natural history section of Laborde was published in 1833, so that the new taxa should be dated to 1833 (and not either 1830 or 1834,

as usually stated, see below), and should be attributed to either "Deshayes, in Laborde, 1833" (mollusks) or "Delile, in Laborde, 1833" (plants). Although Linant was one of the two leaders of the expedition, Linant was neither an author nor an editor of the expedition volume, so that Linant should not be credited in that capacity, contrary to numerous researchers who attributed this work and its new species to "Laborde & Linant."

Laborde's *Voyage*

As this volume was published in a large folio size, 15 × 22 inches (approximately 43 × 59 cm), and natural history comprised less than 10% of the text pages, and only three of 69 plates, it is relatively rare in natural history libraries and was inaccessible to most researchers until recently digitized. Another complicating factor is that while the title page is dated 1830, two of the maps at the end are dated 1833 and 1834, indicating that it was published over a period of three or four years, so that subsequent researchers have variously cited this work as "1830," "1833," or "1834."

The primary purpose of the *Voyage* was to provide a narrative of Laborde's and Linant's travels across the Sinai Peninsula to the archaeologically significant monuments and ruins in Petra, a region that had then been little explored by Europeans (Augé and de Bellefonds, 1990; 1994). The text of the *Voyage* has the following components:

Half-title page, with "explication du frontispiece," two unpaginated pages (1 leaf);
Title page, two unpaginated pp. (1 leaf);
Dedication to "Guillaume II" (William II (1777–1847), Elector of Hesse from 1821 to 1847), two unpaginated pp. (1 leaf, verso blank) [= i–ii];
Preface, two unpaginated pp. (1 leaf) [= iii–iv];
"Introduction" (pp. 1–36);
"Précis du voyage et explication des planches" (pp. 37–72) [page 65 has the text of the molluscan species];
"Cartes de l'Arabie Pétrée – Journal topographique de Suez à l'Accabah" (pp. 73–80);

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"Flore de l'Arabie Pétrée" (pp. 81–87) [page 88 is blank except for the printer's mark]; and

"Liste des planches et indication où elles se trouvent expliquées" (one unpaginated page following page 88).

The book is accompanied by 69 full-page plates as well as a number of text figures. In most of the copies examined, including the online (scanned) version, the 69 plates are bound at the end. One of the two copies in the New York Public Library has the plates interspersed throughout the text, with the plate(s) bound following the specific page on which each plate is cited, with the maps alone at the very end. Plate 1 is of Laborde himself, in "Arabian desert" costume: "Arabe du désert (portrait de l'auteur dans son costume de voyage)." Plates 2 to 62 are archaeological and scenery plates showing various sites in the Sinai and Petra. Plates 63 to 65 are the three natural history plates, devoted to a mammal, the rock hyrax (plate 63), plants (plate 64) and mollusks (plate 65). Plates 66 to 69 are maps of the region, including one showing the routes of earlier expeditions.

The only indications of publication dates in the entire volume are on the title page (dated 1830), Plate 67 (a map with a date of 1833), and Plate 69 (an oversize map not included in the online version, which has a date of 1834). Biographical accounts of Laborde and/or Linant have usually cited this publication as "1830" (e.g., Goby, 1981: 474; Kornrumpf and Kornrumpf, 1998: 219; Kurz and Linant de Bellefonds, 1998: 68; Labib, 1961: 112–116, pls. 13–14; Mazuel, 1937: 99–103); Pfullman (2001: 176–178) cited this as "1830–33," without explanation; Anonymous (1834: 150) stated, without details, that "La publication a eu lieu par livraisons successive de 1830 à 1833."

The key to determining the publication dates is the *Bibliographie de la France*, which Stafleu and Cowan (1976: xxi) described as an invaluable resource, even though, ironically, they did not check it for the dates of Laborde's *Voyage*:

> *Bibliographie de la France* . . . Important source for dating French publications. The weekly issues contain lists of new books, pamflets [*sic*] and of instalments of serial publications. The date on which BF lists a book published in Paris can usually be taken as that of actual publication (Stafleu and Cowan, 1976: xxi).

Fortunately, the *Bibliographie de la France* allows partial reconstruction of the publication history of Laborde's *Voyage*, because it specifies the plate(s) and "feuilles" (leaves, each leaf corresponding to 2 text pages) for this book. The "feuille" numbering is given at the lower right corner of each odd-numbered page, so that page 1 has feuille number 1; page 3 has feuille number 2, and so on (however, the prefatory material and the list of plates do not have feuille numbers).

Interestingly, only some of the plates were issued first in 1830, and the publisher's description as cited in the *Bibliographie de la France* initially stated that a separate, smaller octavo-size text volume would follow. Instead, the text was ultimately published in 1833 in the same large folio size as the plates. As set forth below, this source confirms that 29 plates were published in 1830, while at least 31 plates and text pages 1–88 were published in 1833:

Bibliographie de la France	Date	Laborde, *Voyage*
19(4): 89	23 January 1830	Livraison 1, 4 pls.
19(10): 157	6 March 1830	Livraison 2, 5 pls.
19(16): 251	17 April 1830	Livraison 3, 5 pls.
19(21): 333	22 May 1830	Livraison 4, 5 pls.
19(29): 490	17 July 1830	Livraison 5, 5 pls.
19(38): 626	18 September 1830	Livraison 6, 5 pls.
22(32): 499–500	10 August 1833	Livraisons 7–9, feuilles 1–18 [= pp. 1–36]; 12 pls.
22(48): 757	30 November 1833	Livraisons 10–12, feuilles 19–44 [= pp. 37–88 and preface; list of plates(?)]; 19 pls.
No further citations	n/a	[9 pls.; title pages (?)]

However, further confusing matters is that the plates were not numbered when they were issued, nor were the plates issued in the same sequence as they were finally numbered. Instead, the plates were not numbered until 1833, with the issuance of the list of plates, which required the purchasers to re-arrange the plates in the correct numerical sequence, and (some) purchasers then hand-numbered the plates before having them bound in the correct sequence.

In an "Avis" (guide) to the reader, inserted in one of the copies in the Library of Congress, the publisher provided an explanation for the delay in publication and a listing of the plates in Livraisons 10, 11, and 12 (Anonymous, 1833). The publisher wrote: "M. Collin, graveur distingué … étant tombé malade fut force d'interrompre ses travaux; il n'a pa les reprendre que dupuis peu de temps et ne pourra les terminer que vers la fin de l'année" [Mr. Collin, a distinguished engraver, became sick and was obliged to interrupt his labors; he has not been able to resume them until recently, and cannot finish them until the end of the year].

The "Avis" provided details on the contents of Livraisons 10 to 12, with the caveats that the listing of plates in the "Avis" does not include the plate number, and the description of each plate in the "Avis" does not always match the actual title of the plate in the final "list of plates" – but the "Avis" does confirm that the three natural history plates (63, 64, and 65) were issued in 1833:

Livraison 10	"Dédicace; Six feuilles de texte" [pp. 37–48]	6 plates (including what are now plates 5, 6, 46, 47, either 57 or 58, and 63).
Livraison 11	"Douze feuilles de texte" [pp. 49–72]	8 plates (including what are now plates 1, 4, 5, 31, and 64).
Livraison 12	"Préface et table; Huit feuilles de texte" [pp. 73–88]	7 plates (including what are now plates 10, 11 or 12, 25, 53 or 55, 65, 66, and 68).

The listing of plates in the "Avis"—21 plates for Livraisons 10 to 12—is inconsistent with the *Bibliographie de France*, which indicates only 19 plates for those Livraisons, suggesting that two plates listed in the "Avis" were not issued until 1834.

Vicaire (1900: 758–759) cited the *Bibliographie de la France* in noting that this was issued in 12 livraisons from 1830 to 1833, but did not notice that there had to be at least one more Livraison (for nine of the plates), or that the oversize map was dated 1834. Augé and de Bellefonds (1994: 20–21) briefly discussed the publication history of the *Voyage*, and stated that the last text section on botany (pp. 81–87) was sent to subscribers in 1833, with the oversize map (pl. 69) being sent in 1834: "la dernière livraison, comprenant la *Flore de l'Arabie Pétrée*, par M. Delille [*sic*], est envoyée aux souscripteurs en 1833, et un grande *Carte de l'Arabie* vient même s'y ajouter en 1834."

In most copies of the work that we have seen, the three natural history plates are in black and white, as are the remaining archaeological and anthropological plates. We have seen several copies (including the scanned copy from the Bibliothèque Nationale de France, Paris) in which plate 63, illustrating the rock hyrax, a desert mammal [*Procavia capensis* (Pallas, 1766)], is colored. In addition, of the three copies currently for sale through AbeBooks.com (last viewed on 10 May 2019; average price $34,182 or €29,977), all have plate 63 colored, but none have plate 65 colored (B. El Hage, in litt. 15 Jan. 2019; C. Frey, in litt. 16 Jan. 2019; S. Thompson, in litt. 15 Jan. 2019); the copy recorded for sale by Maggs in 1989 was similarly listed as having "1 [plate] coloured by hand" (Navari, 1989: 196 –197). The catalogue of Deshayes' own sizable library (which was auctioned shortly after his death) indicates that he only had Livraisons 1–5 (i.e., 24 plates), but not the text or the remaining plates, which means that he did not even have a complete set of this work (Anonymous, 1875: 16). We have learned of only two copies (both in Washington, D.C., at Dumbarton Oaks and the Library of Congress) in which plate 65, of the mollusks, is also colored. Yaron (1979: 248) also saw a copy with plate 65 colored, but he did not indicate which library owned it (presumably in Europe). Given the rarity and the scientific value of the colored version of plate 65 for identifying the molluscan species, we have republished it here (Figure 1) in roughly half its original size. Some of the plates have bilingual English-French captions, and others have titles in French alone; plate 65 is labeled in both languages, "Coquilles de la Mer Rouge / Schells [*sic*] from the Red-Sea."

The narrative and archaeological sections of the *Voyage* were soon translated into English with additional Biblical commentary, but the translation did not include the natural history sections (Anonymous, 1836, 1838).

"*Coquilles de la Mer Rouge*"

The list of the Red Sea mollusks by Deshayes, essentially a plate explanation without formal descriptions, appears on page 66, which is the second page of feuille 33 (published by November 1833), and the specimens were then illustrated on plate 65 (published in 1833, because plate 67 has an 1833 date). Seventeen species of marine mollusks, thirteen of them new, all from the northern Red Sea, are listed, the majority only by citation to the illustration, i.e., "name and figure only", some with brief notes about similar species but few if any with sufficient information to provide availability absent the illustrations. Plate 65 does not have any taxonomic names printed on the plate or on a separate plate caption sheet. Pursuant to ICZN *Code* Recommendation 51E (ICZN *Code*, 1999), these taxa should be cited as "Deshayes, in Laborde, 1833." Because the map of the expedition indicates that Laborde and Linant traveled along both eastern and western coasts of the Sinai Peninsula, the type locality of these species should be "northern Red Sea" as it cannot be determined whether the specimens were collected in the Gulf of Aqaba, the Gulf of Suez, or both.

The shells on Plate 65 were drawn by Paul Louis Oudart (1796–1860), a French artist best known for his drawings of birds and flowers (Bellier de la Chauvignerie, 1885: 180; Nissen, 1953: 48, 194; 1967: 238; 1978: 573; Bischoff, 2015). Oudart also did some of the illustrations for Deshayes' first monograph on Cenozoic fossil mollusks from outcrops near Paris, the *Descriptions des coquilles fossils des environs de Paris* (Deshayes, 1824–1837) (Nissen, 1966: 116).

Based on review of the malacological literature over the past century, fourteen (14) publications have used "1830" as the date for the new species, fifty-four (54) publications have used "1834" as the date, and we have not found any that used 1833 as the correct date. Houart and Tröndlé (2008: 86, 88) explained their determination that 1834 should be used, but later in the same paper used "Deshayes, 1833" in a table (2008: 93), which while correct as to the year was unintentional. There are also numerous permutations of the authorship: 25 publications attributed this to Deshayes alone; 3 to Laborde alone; 10 correctly to Deshayes, in Laborde; 2 to Laborde and Deshayes; 1 to Deshayes, in Laborde and Deshayes; and 27 to Deshayes, in Laborde and Linant.
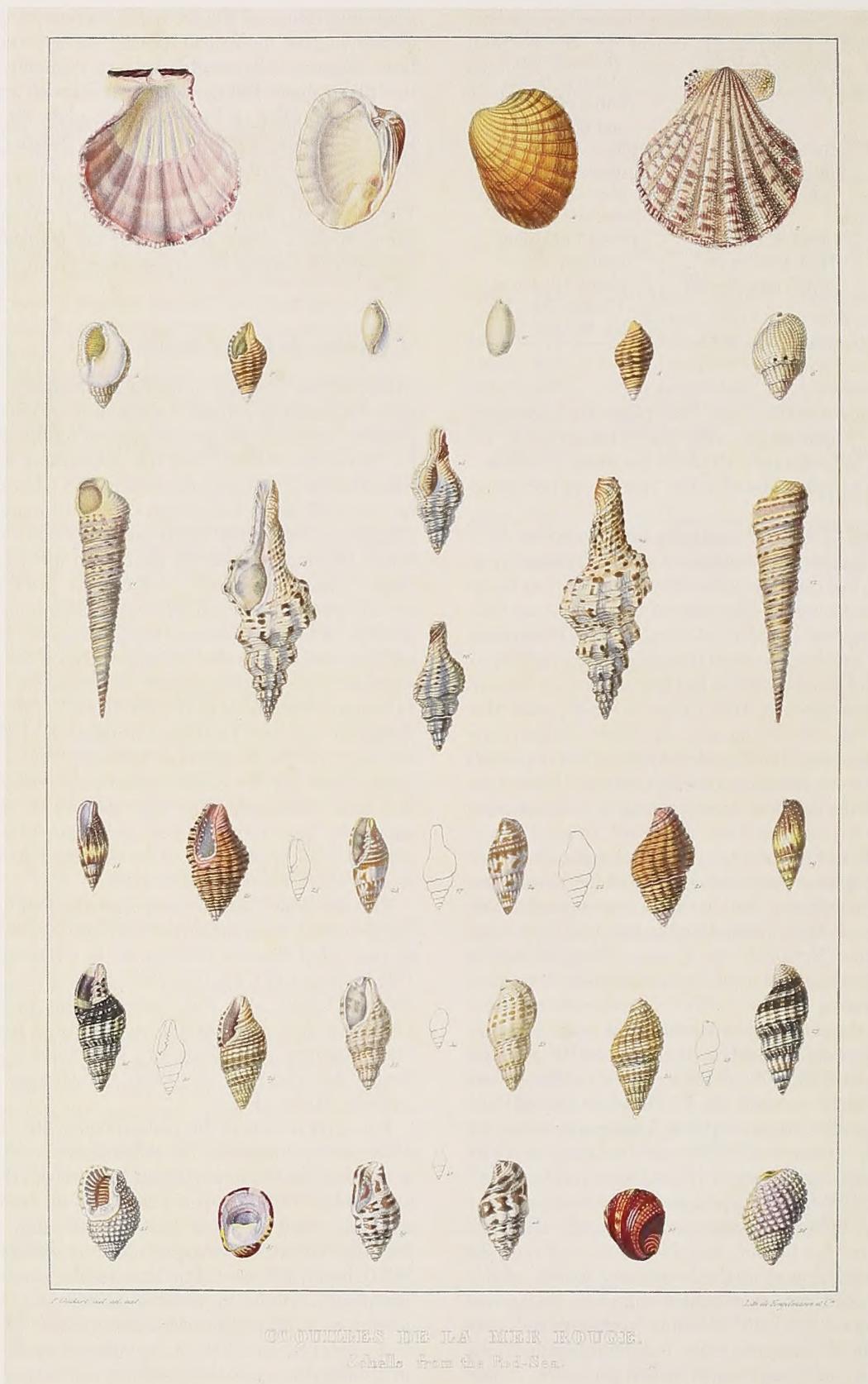
Figure 1. Reprint of Plate 65 from Laborde (1833), reduced from the original size (15 × 22 inches, circa 43 × 59 cm). Reproduction © Dumbarton Oaks Research Library and Collection, Rare Book Collection, Washington, D.C.

Three malacological publications have discussed this publication and its new taxa as a whole. The first was Lamy (1927), who used a manuscript by Félix Pierre Jousseaume (1835–1921), as well as the literature on the mollusks of the Red Sea, as the basis for determining the then-current identity of these taxa. Lamy erred by attributing the species to Laborde alone and by dating them all to 1830.

Shortly thereafter, Tomlin and Salisbury (1928), not having seen or cited Lamy's paper, independently reanalyzed the molluscan taxa. They noted that two of the maps "bear dates 1833 and 1834, so that the book could not have been published prior to this last date, in spite of the date on the title page, which is given as 1830," and stated that "the names should be credited to Laborde and Deshayes" (Tomlin and Salisbury, 1928: 32). Meanwhile, Sherborn (1925: cxxxviii; 1932: cxl) attributed the species to "Deshayes in Laborde, 1830."

Subsequently, Yaron (1979) compared the results of Lamy (1927) and Tomlin and Salisbury (1928), noting that the two publications "arrived at practically identical conclusions with regard to the identity of most of Laborde's species" (Yaron, 1979: 248). Yaron erred, however, in listing Linant as a co-author, by using "Deshayes in Laborde and Linant, 1834" for the new species. Yaron (1979: 252) concluded that at least three, and possibly four of the new species were still accepted as valid, with the remaining species either junior synonyms or junior homonyms.

Based on our review of the subsequent literature, it appears that of the 14 "new" species, one was actually first described by Brocchi (1814); seven are currently accepted as valid, five are junior synonyms (one of which is also a junior homonym), and one is a *nomen dubium*. Although this was not the first description of mollusks from the Red Sea—that honor belongs to Peter Forsskål and Carsten Niebuhr who collected there in the 1760—and several other expeditions also collected mollusks in the Red Sea in the ensuing decades (Issel, 1869: 4–12; Yaron et al., 1986), it is a useful benchmark for the northernmost Red Sea.

Interestingly, of the twelve currently available species (or their senior synonyms), four are endemic to the Red Sea and the adjacent Gulf of Aden, another four are limited to the Red Sea and the western Indian Ocean, and the remaining four have a broader Indo-Pacific distribution. This is consistent with the high degree of endemicity of the marine molluscan fauna of the Red Sea. Dekker and Orlin (2000: 4) concluded that "16% of the Red Sea species are endemics," not including the poorly studied Triphoridae, Eulimidae, Epitoniidae, and Pyramidellidae. Subsequently, Dekker estimated that the endemicity of the Red Sea molluscan fauna is in the range of 20% to 25% (H. Dekker in litt., 11 Feb. 2019).

We provide an annotated catalog of the molluscan taxa, including references to the secondary literature, emphasizing the Red Sea literature (for several widespread species that have been extensively cited, the citations are a representative sampling). Syntypes or potential syntypes, housed in the Muséum National d'Histoire Naturelle (Paris), are known for only two of the species.

Bivalvia

pictus, Pecten – 1833: 66, pl. 65, figs. 1–2. Junior homonym of *Pecten pictus* da Costa, 1778. Deshayes' species is now known as *Gloripallium maculosum* (Forsskål, 1775) (Dekker and Orlin, 2000: 10; Dijkstra and Knudsen, 1998: 61–63, pl. 6, fig. 28), endemic to the Red Sea and Gulf of Aden [Pectinidae].

rufa, Cardita – 1833: 66, pl. 65, figs. 3–4. *Cardites rufa* (Deshayes, in Laborde, 1833) (Oliver, 1992: 115–116, pl. 24; Dekker and Orlin, 2000: 12; Mienis, 2000: 131; Rusmore-Villaume, 2008: 224–225), with a female ending on this male genus; or more correctly *Cardites rufus* (Deshayes, in Laborde, 1833) (Huber, 2010: 654), endemic to the Red Sea [Carditidae].

Gastropoda

biangulatus, Fusus – 1833: 66, pl. 65, figs. 13–14. Synonym of *Fusinus undulatus* (Gmelin, 1791). Possible syntypes, MNHN-IM 2000-6469; however, "The two alleged syntypes of [the] Deshayes species … housed in the MNHN collection … are probably not conspecific with that species" (Snyder, 2006: 107), Indo-Pacific [Fasciolariidae].

candidula, Bulla – 1833: 66, pl. 65, fig. 9–10. Synonym of *Atys cylindricus* (Helbling, 1779) (Yaron, 1979: 249), now *Aliculastrum cylindricus* (Helbling, 1779) (Too et al., 2014: 357, 362), Indo-Pacific [Haminoeidae].

depexa, Mitra – 1833: 66, pl. 65, figs. 23–25. *Vexillum (Pusia) depexum* (Deshayes, in Laborde, 1833) (Cernohorsky, 1970: 56; Mienis, 1985; 2004; Dekker and Orlin, 2000: 30; Turner, 2001: 28; Rusmore-Villaume, 2008: 120–121), endemic to Red Sea; introduced into eastern Mediterranean. Dekker (1993: 3) determined that the specimen illustrated by Sharabati (1984: 66, pl. 26, fig. 3) of this species is instead *Vexillum microzonias* (Lamarck, 1811). [Costellariidae].

fasciolaris, Mitra – 1833: 66, pl. 65, figs. 18–19. *Mitra fasciolaris* Deshayes, in Laborde, 1833 (Cernohorsky, 1970: 35; 1976: 320–321, pl. 255, figs. 12–13, pl. 272; Sharabati, 1984: 66, pl. 26, fig. 1; Bosch et al., 1995: 149, fig. 625; Dekker and Orlin, 2000: 29; Rusmore-Villaume, 2008: 116–117), now *Strigatella fasciolaris* (Deshayes, in Laborde, 1833) (Fedosov et al., 2018: 301), endemic to the Red Sea [Mitridae].

festiva, Columbella – 1833: 66, pl. 65, figs. 39–41. *Euplica festiva* (Deshayes, in Laborde, 1833) (Drivas and Jay, 1997: 28; Dekker and Orlin, 2000: 28; Rusmore-Villaume, 2008: 102–103), Red Sea and western Indian Ocean [Columbellidae].

incarnata, Turbinella – 1833: 66, pl. 65, figs. 20–22. *Engina incarnata* (Deshayes, in Laborde, 1833) (Cernohorsky, 1971: 160–162, 164, figs. 80–81; 1975: 183, fig. 17); *Clivipollia incarnata* (Deshayes, in Laborde, 1833) (Dekker and Orlin, 2000: 27; Rusmore-Villaume, 2008: 100–101; Fraussen and Stahlschmidt, 2016: 33–34, figs. 3F–H, 6G–L), restricted to Red Sea and western Indian Ocean. Syntype, MNHN-IM 2000-30244 (figured, Fraussen and Stahlschmidt, 2016: fig. 6I-J) [Pisaniidae].

leucozonias, Mitra – 1833: 66, pl. 65, figs. 26–28. *Mitra (Costellaria) leucozonias* (Deshayes, in Laborde, 1833) (Lamy, 1938: 47); or *Vexillum (Costellaria) leucozonias* (Deshayes, in Laborde, 1833) (Cernohorsky, 1970: 55; Ladd, 1977: 64, pl. 20, fig. 11; Kay, 1979: 321, fig. 107-C; Turner, 2001: 41; Severns, 2011: 302–303, pl. 134, fig. 3); or *Vexillum leucozonias* (Deshayes, in Laborde, 1833) (Sharabati, 1984: 68, pl. 27, fig. 5; Dekker and Orlin, 2000: 30; Rusmore-Villaume, 2008: 122–123), Indo-Pacific [Costellariidae].

obvelatum, Buccinum – 1833: 66, pl. 65, fig. 5–6. Synonym of *Nassarius arcularia plicatus* (Röding, 1798) (Cernohorsky, 1984: 57–58); or *Nassarius obvelatus* (Deshayes, in Laborde, 1833) (Dekker and Orlin, 2000: 28), Red Sea and Persian Gulf to South Africa [Nassariidae].

pauperculus, Fusus – 1833: 66, pl. 65, figs. 15–17. Status uncertain: Lamy (1927: 380) noted that previous authors had doubtfully compared this with *Fusus strigatus* Philippi, 1850, and *F. tuberculatus* Lamarck, 1822; Tomlin and Salisbury (1928: 33) stated that this was "A *Murex*, but hardly determinable", which Snyder (2006: 158 and 275) followed. If this species is a "*Murex*" then it would be a senior secondary homonym of *Murex pauperculus* C. B. Adams, 1850 (a widely cited Caribbean species now placed in *Dermomurex*). However, as Deshayes' name has not been used as an available species, it is here regarded as a *nomen dubium*.

serriale, Buccinum – 1833: 66, pl. 65, figs. 32–34. *Maculotriton serriale* (Deshayes, in Laborde, 1833) (Cernohorsky, 1972: 129–130, pl. 36, fig. 11; Salvat and Rives, 1975: 317, fig. 217; Cernohorsky, 1982: 130–134, figs. 22–30; Tröndlé and Houart, 1992: 90–91, figs. 51–56; Wilson, 1994: 23; Bosch et al., 1995: 121, fig. 482; Houart, 1995: 263–264, fig. 87; Higo et al., 1999: 209; Dekker and Orlin, 2000: 27; Houart, 2008: 200, pl. 395, fig. 1; Houart and Tröndlé, 2008: 86, 88; Rusmore-Villaume, 2008: 92–93; Spencer et al., 2009: 210; Tröndlé and Boutet, 2009: 28; Houart et al., 2010: 265; Severns, 2011: 280–281, pl. 123, fig. 8; Claremont et al., 2013: 21; Tan and Low, 2014: 354; Okutani, 2017: 956, pl. 249, fig. 8) (and numerous other publications), Indo-Pacific. Several authors have erroneously emended the species name to "*serrialis*" (*e.g.*, Satyamurti, 1952: 161–162; Asakura et al., 1993: 12; Apte, 1999: 346; Lee and Chao, 2003: 34, 42, pl. 4, fig. 21; Smith, 2003: 260). Cernohorsky (1982: 132,

fig. 22) designated Deshayes' illustration as the lectotype of this species [Muricidae].

teniata, Turbinella – 1833: 66, pl. 65, fig. 7–8. Synonym of *Latirus turritus* (Gmelin, 1791) (Tomlin and Salisbury, 1928: 33; Snyder, 2003: 204), now *Turrilatirus turritus* (Gmelin, 1791) (Vermeij and Snyder, 2006: 419), Red Sea and western Indian Ocean [Fasciolariidae].

vermicularis, Turritella "nob." – Lamy (1927: 380) attributed this species to "Laborde" (i.e., Deshayes, in Laborde, 1833: 66, pl. 65, figs. 11–12), but Deshayes cited *Turbo vermicularis* Brocchi (1814: pl. 6, fig. 13), which is now *Helminthia vermicularis* (Brocchi, 1814) (Landau et al., 2013: 62–64, pl. 5, fig. 11), so Deshayes' usage was a new combination, not a new species. Deshayes stated that this material was the Recent analog of Brocchi's fossil species ["l'analogue vivant de la coquille fossile figurée par Brocchi"], so that Deshayes' usage of "Nob." [*nobis* or new] for this species would now be seen as inappropriate, but he and others of his time often did this on the transfer of an earlier author's species to a different genus. However, Brocchi's species is limited to the Early Miocene to Early Pleistocene of the Mediterranean, and is not known from the Recent (Landau et al., 2013: 64), so Deshayes' material may be referrable to another species of (Recent) Turritellidae from the Red Sea [Turritellidae].

"*Flore de l'Arabie pétrée*"

Alire Raffeneau-Delile (1778–1850) authored the botanical section of the *Voyage*, titled "Flore de l'Arabie pétrée," printed on pages 81–87 and accompanied by plate 64. Delile, a professor at Montpellier, was best known for his publications of the botany of Egypt, issued as part of the *Description de l'Égypte* in two editions from 1812 to 1829 (Motte, 1971; Rioux, 2014: 334–336; Stafleu and Cowan, 1976: 617). Delile was thus a logical choice to describe the plants collected by Laborde and Linant, and his text included a description of 85 species, of which eight are new. Plate 64 has illustrations of six of the new species.

However, Delile must have realized that the folio size of the *Voyage* and its focus on geography and archaeology would limit the distribution of his botanical chapter, as he had the entire botanical section reprinted and re-typeset in a smaller quarto size, titled "*Fragments d'une Flore de l'Arabie Pétrée: plantes recueillies par M. Léon de Laborde*" (Delile, 1833).

The botanical literature has used either 1830 or 1833 as the date for Delile's section. Pritzel (1872: 79) correctly dated the "*Fragments*" version to 1833, but incorrectly dated the original Laborde version as 1830. This error was repeated by Stafleu and Cowan (1976: 617) who wrote: "The original text, in folio, appeared in 1830, p. 81–87 (fide PR)," citing Pritzel. Jackson (1881: 379) dated the "*Fragments*" version to 1833, but made no mention of the original Laborde version. Rioux (2014: 338) dated the Laborde version as 1833 and illustrated the title page of the "*Fragments*" version, but did not further discuss

either version. Embacher (1882: 180), an encyclopedia of travel books, dated the entire *Voyage* as 1830–33, and the "Flore de l'Arabie pétrée" to 1833; the latter being Delile's reprint. Joly (1859: 95–96) correctly dated the "*Fragments*" to 1833, and noted that there was an unpublished second part, "*Nouveaux fragments d'une Flore de l'Arabie Pétrée: plantes recueillies aux environs du mont Sinaï par M. le baron Taylor*", prepared in April 1834 to be presented to the Académie des Sciences, Toulouse. As noted above, Augé and de Bellefonds (1994: 20–21) explained that the botany section of the *Voyage* was sent to subscribers in 1833, which should be used as the publication date for both the *Voyage* version and the "*Fragments*" version. The botanical section thus confirms the 1833 publication date for the molluscan taxa.

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Crepidula fornicata (Linnaeus, 1758) (Gastropoda: Calyptraeidae) as a hermit crab commensal in the North Sea

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ABSTRACT

The association of *Crepidula fornicata* (Linnaeus, 1758) with hermit crabs is discussed, based on recent observations from the coast of Zuid-Holland (The Netherlands). In the Netherlands, the species is a generalist that occupies a wide range of substratum types, but at the investigated localities it is most frequent on hermit-crab occupied gastropod shells, in particular those of *Euspira catena* (Da Costa, 1778). For the first time a number of specimens is reported that has *C. fornicata* not only on the outside, but also on the inside of the aperture, to which it adapts its shell shape.

INTRODUCTION

In the late 19th century, *Crepidula fornicata* (Linnaeus, 1758) was introduced, via oysters, from the East coast of North America to the United Kingdom, from where it spread throughout the North Sea (living specimens were first recorded from the Netherlands in 1929; Wolff, 2005). In the Netherlands it became abundant in the delta and in the Wadden Sea, where it mainly grows on oysters and mussels (De Bruyne et al., 2013). Thieltges et al. (2002) studied a part of the German Wadden Sea where they made the same observation, but also found that in subtidal areas it relies on other substrates, mainly provided by *Buccinum undatum* (Linnaeus, 1758). In that area, about 70% of *C. fornicata* occur on *B.undatum* shells occupied by hermit crabs, 14% on dead *B.undatum*, 2% on living *B.undatum*, and the remaining 14% on crabs (*Cancer pagurus* Linnaeus, 1758). In its native range, Karlson and Shenk (1983: table 3) even found a greater preference for shells occupied by hermit crabs (compared to empty shells). The preference to settle on shells occupied by hermit crabs is explained by the longer time to grow and develop as larger species of hermit crabs prevent their shells from being covered by sediment or buried in the substratum, provide increased food supply due to mobility of the crab and water currents set up by its feeding, and provide protection from predators (Conover, 1975, 1979).

Along the coast of the province Zuid Holland, an area with a sandy sea bed that does not provide a suitable substrate for *Crepidula fornicata*, only small numbers of beached specimens were observed until recently. These were always attached to shells (own observations since mid-1970s). After storms in the winters of 2017 and 2019, large numbers of marine organisms washed up (e.g., Raven, 2017) including the bivalve *Mytilus edulis* (Linnaeus,1758), of which dozens with *C, fornicata* and hundreds of specimens of the gastropod *Euspira catena* (Da Costa, 1778). The latter were partly alive, partly fresh-dead shells occupied by hermit crabs and with *Crepidula fornicata*. Previously, only old (often blue-tinted) Holocene specimens of this gastropod washed up, which indicates that (like several other species) it now lives closer to the coast (Raven, 2017). Their typical collar-shaped egg capsules also frequently wash up on the same beaches (own observations). As *Euspira catena* lives buried in the sand, the smooth shells of the living specimens have no epibionts. Upon death of the mollusk, the shell quickly becomes covered by all kinds of organisms, especially when a hermit crab (*Pagurus bernhardus* (Linnaeus, 1758)) occupies the shell: these are mostly barnacles, sea mat *Hydractinia echinata* (Fleming, 1828), and the subject of this paper: *C. fornicata*.

In the Netherlands, *Crepidula fornicata* has been observed to occupy a wide range of substratum types: on large stones, on living bivalves (especially the Mussel *Mytilus edulis* (Linnaeus, 1758), and the Pacific oyster *Magellana gigas* (Thonberg, 1793)), inside empty bivalves (e.g., *Acanthocardia echinata* (Linnaeus, 1758), Figure 4), on shells inhabited by hermit crabs, etc. It thus is a facultative commensal of hermit crabs, living on the outside of the shell (also noted by Conover, 1976; Williams and McDermott, 2004). This agrees to the general behavior reported for this species (Anonymous, 2019). Vermeij (1989) reported *Grandicrepidula grandis* (Middendorff, 1949), which occupies the full range of substratum types that in other regions are occupied by three or four more specialized calyptraeids, including the interior surfaces of gastropod shells occupied by hermit crabs.

The compelling reason that drove me to embark on this research is that several specimens not only had *Crepidula fornicata* on the outside, but also inside the aperture. Only a single unpublished record of this behavior has been found, although the literature about hermit crabs and their commensals is vast and other observations could be buried in a more generic paper on this subject.

MATERIALS AND METHODS

This work is based on observations by the author at various localities in the Netherlands over a period of more than 40 years, but key input is from material that washed up along the coast of Zuid-Holland after storms during the winters of 2017 and 2019. During each visit to Scheveningen and Hoek van Holland (Figure 1) about 3 km of shoreline were inspected for 2 hours. All gastropods with *Crepidula fornicata* inside the shell were collected, as well as some specimens with *C. fornicata* only on the outside. Numbers of shells observed were estimated. The collected shells were photographed, cleaned and re-assembled. All material is kept in the author's collection. Abbreviations: L = length, H = height, W = width. These were measured using a digital caliper. For shell height, the protruding septum (Figures 11c, 17c) was included in the measurement.

RESULTS AND DISCUSSION

All shells inhabited by hermit crabs are *Euspira catena*, in addition to a single, gerontic *Buccinum undatum* Linnaeus, 1758. Both species have large shells (compared to others in the local fauna) with wide apertures. Several shells were found with *Crepidula* but no hermit crab; the crab may have died before, have washed out during transport to the beach, or abandoned the shell. Hermit crabs often change shell as they grow or if epibionts make the shells too heavy or unstable (e.g. Conover, 1979).

All shells found with hermit crabs had *C. fornicata* on them, which indicates how successful its larvae are in finding shells occupied by hermit crabs. *Crepidula fornicata* grows fast: two months after settling they can be 4 mm long and sexually mature as females (Walne, 1956). This could be an advantage as it allows the animal to grow and reproduce before the hermit crab abandons the shell (Conover, 1979). Once a single *C. fornicata* is present, more will follow; either they settle on the first specimen or next to it. As more specimens settle, the *Crepidula fornicata* form stacks (see Figure 3 for rather long stacks). In such stacks, the oldest specimens are female, the youngest are male, those in between are protandrous hermaphrodites; as the stack grows specimens will change sex (e.g., Fretter and Graham, 1981; Collin, 2006).

As the oldest specimen in a stack dies it becomes disconnected from its substratum but the stack will survive. Frequently such stacks are found with an overgrown and/or eroded specimen at its base. As the individual *Crepidula fornicata* and the stacks grow, their weight or weight distribution can become a serious burden for the host (e.g. Figure 3) and the crab may abandon the shell (Conover, 1978). In several of the shells with larger *C. fornicata* no hermit crab was present (e.g., Figures 3, 7, 10), but it is assumed the stacks started on a hermit crab-inhabited shell.

On a few female shells two or three males were present (e.g., Figures, 7, 8). Only in one case a female had multiple stacks on it. *Crepidula fornicata* observed left a clear mark on the host shell. Some host shells were found with such marks indicating that a *C. fornicata* (or stack of such shells) had
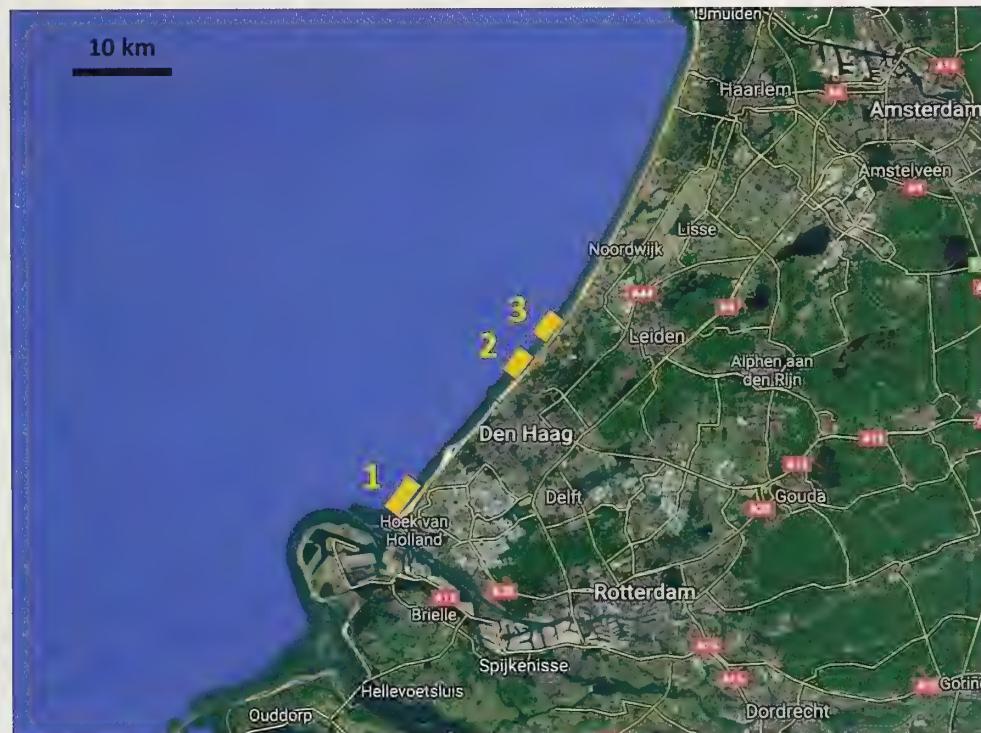
Figure 1. Location map. 1. Hoek van Holland. 2. Northern Beach, Scheveningen. 3. Wassenaarse Slag, Wassenaar. Source: Google Maps.
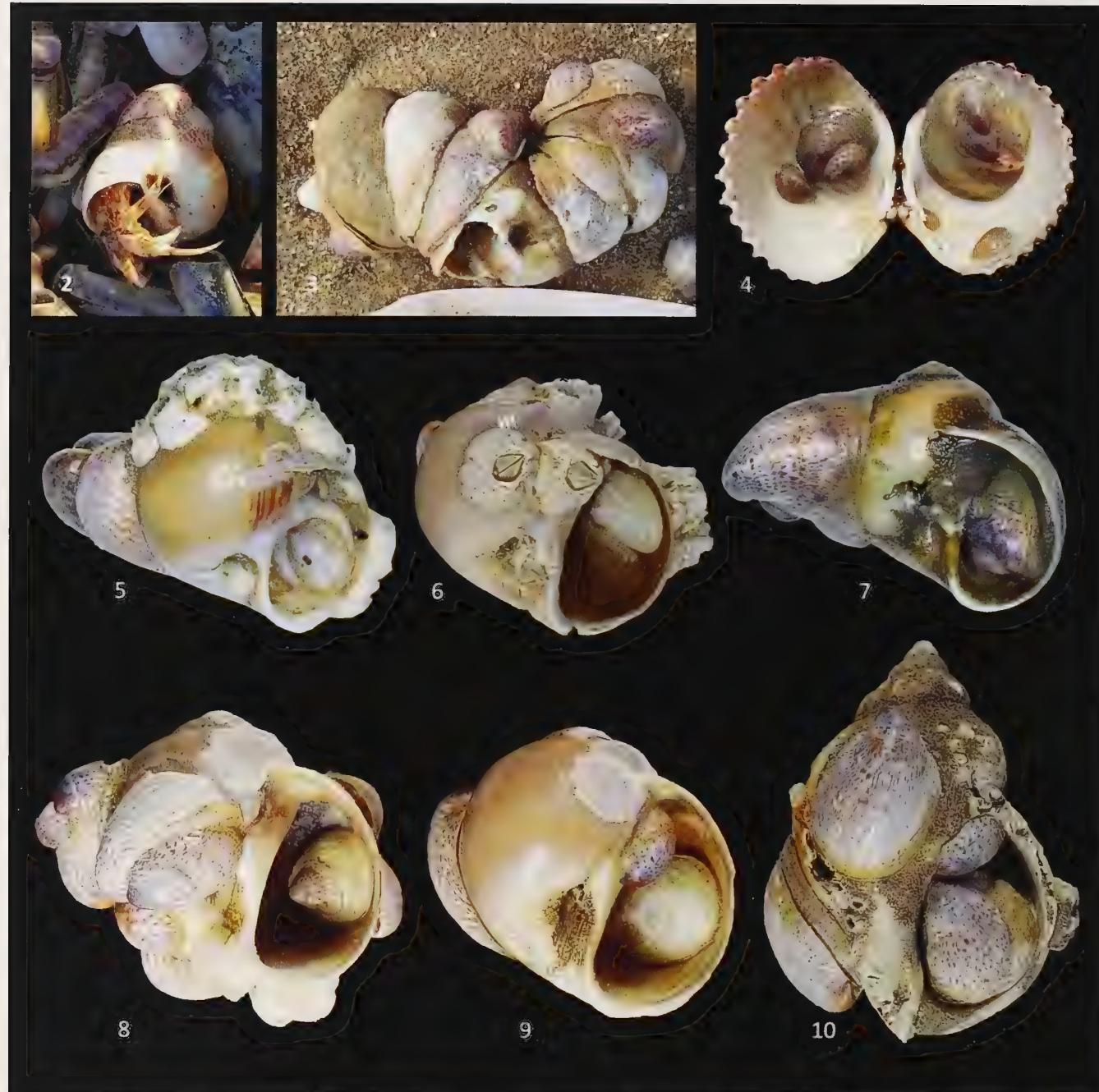
Figures 2–10. Hermit crab-inhabited shells with *Crepidula fornicata*. **2.** *Euspira catena* (H ~35 mm) with hermit crab and with *C. fornicata* on outside, Scheveningen, Jan. 2017. **3.** *Euspira catena* with two long and complex stacks of *Crepidula fornicata* on outside, some with sea mat or barnacles, Wassenaarse Slag, Wassenaar, March 2019 (total W ~10 cm). **4.** *Acanthocardia echinata* (L = 40 mm) with two stacks and three individual *Crepidula fornicata* inside, Hoek van Holland, Feb. 2019. Note the "flatness" of the female in the valve on the right. **5–6.** *Euspira catena* with *C. fornicata* on outside and inside aperture, Scheveningen, Jan. 2017. **5.** *Euspira catena* (H ~ 35 mm) (Table 2: 1). **6.** *Euspira catena* (H = 33 mm) (Table 2: 3). **7.** *Euspira catena* (H = 38 mm) with *C. fornicata* stacks on outside and inside the aperture, Hoek van Holland, Feb. 2017 (Table 2: 4). **8.** *Euspira catena* (H = 35 mm) with several stacks of *Crepidula fornicata* on the outside and another stack inside the aperture, Hoek van Holland, Feb. 2019 (Table 2: 9). **9.** *Euspira catena* (H = 38 mm) with *C. fornicata* stacks on outside and inside the aperture, also in adapical position, Hoek van Holland, Feb. 2019 (Table 2: 11). **10.** *Buccinum undatum* (H = 62 mm) with large *Crepidula fornicata* on outside and inside the aperture, also in the adapical position, Hoek van Holland, Feb. 2019 (Table 2: 14). Note the profuse presence of boring sponges, sea mat, barnacles and bryozoans that died some time ago.

been present but dropped off (e.g. Figure 16). As the specimens studied were transported during a storm it is likely the *C. fornicata* were lost as result of the transport to shore, rather than by death in deeper water. The marks are informative in the re-assembly of host shells and their commensals (in addition to the photos taken before cleaning), but the marks appear not to be preserved in fossils (Walker, 1992). *Crepidula fornicata* fit precisely onto the host shell or underlying *C. fornicata*, but in stacks with overlapping shells a narrow slit may be left open. It was noted that the commensals are generally (not always) oriented with their head toward the aperture of the host shell; this suggests that they could benefit most from the water currents produced by the host and are closest to their food leftovers.

In January 2017, at Scheveningen and Hoek van Holland several specimens were found with *Crepidula fornicata* inside the aperture—the first ones recorded (Tables 1 and 2). Where specimens on the outside are convex and rather dark colored due to the presence of numerous brown spots, the females on the inside are quite flat and predominantly white or pale colored (compare Figures 11–15 with Figure 10). Their outline reflects the inside of the last whorl of the host shells, and being flat most likely minimizes hindrance resulting from movements of the host. In many specimens on the inside a short stack formed with one to two specimens on top of the female. Those are typically more globose (Figures 5, 7, 10, 11) and may be darker colored, not only as juveniles (Figure 7), but also as adults (e.g., Figure 10). As the commensals grow there soon will be no space left for the host. Some shells were found with such large *C. fornicata* inside that indeed no space was available for a host (Figures 7, 10). It remains uncertain whether growth of the commensals eventually killed the host, whether the host died by natural cause, but more likely it just moved to another shell. In any case, the commensals on the outside and inside survived. These were always shells that have been occupied, apparently for some time, by a hermit crab, as evidenced by the large size of *Crepidula fornicata*, the presence of a large number of boreholes from boring sponges, and remains of barnacles and hydrozoans (see also Table 2).

When living inside gastropod shells occupied by hermit crabs, *Crepidula fornicata* has a flat shell (H max. = 6.3 mm; H/L ratio = 0.21 to 0.31 or 0.24 ± 0.032 (n= 11)) having its head oriented towards the opening.

Some specimens also had a small specimen in a position not noted before: on the adapical side of the aperture of the host shell (e.g. Figures 5, 9, 10), in one case a stack of two. These specimens are always convex and dark colored. They occur on shells with or without *Crepidula fornicata* on the inside.

As mentioned above, *C. fornicata* is a generalist, but unlike *Grandicrepidula grandis* it has thus far not been reported from the interior surfaces of gastropod shells occupied by hermit crabs (Vermeij, 1989). The only evidence that was found of *C. fornicata* living inside a shell is a photograph on a website (Krisberg, 2011) of both *C. fornicata* and *C. plana* Say, 1822 inside the aperture of *Sinistrofulgur sinistrum* (Hollister, 1958) from Fort Pierce Inlet (Florida). Although there is no mention of a

hermit crab being present, the presence of very flat *Crepidula fornicata* inside the aperture suggests that the shell must have been occupied by a hermit crab (Walker, 1989), but the overgrowth indicates the shell had been abandoned for some time. Interestingly, these *Crepidula fornicata* are flat, despite the aperture being very large. Vermeij (1989) concluded his paper stating: "It will be interesting to determine whether *C. fornicata* in Europe occupies the interior surfaces of hermit-crab shells, a habit rarely if ever occupied by *C. fornicata* in its native American range."

This question can now be answered: yes, it does. Specimens of *Crepidula fornicata* living inside the aperture are very flat and white or pale-colored, and thus are similar to *Crepidula maculosa* Conrad, 1846. However, the sinuate septum and the protoconch of one whorl (when preserved) demonstrate we are not dealing with a new American immigrant (a good comparison between the two species is provided by Krisberg (2009). Numerous other calyptraeids that live mainly inside hermit-crab occupied gastropods are flat and white, such as the slipper limpet *Ergaea walshi* (Reeve, 1859) (own observations in northwestern Borneo; Figures 17–18) and the species of the *Crepidula plana* species complex in North America (Collin, 2000).

Ergaea walshi benefits from its association with hermit crabs through increased food supply, reduced predation, and (in the northern part of its range) extended breeding season due to host migration to more suitable environments during winter (Yipp, 1980). Yoshikawa et al. (2018) describe how the commensal prefers hermit-crab occupied shells with wide aperture, which it finds by selecting larger hermit crabs. Even so, it has to limit its thickness to a maximum of about 5 mm to not be hindered by the movements of the hermit crab (note Yoshikawa et al. (2018) exclude the septum from the measurement of shell height). It thus has the flattest shell of 23 species of Calyptraeidae they investigated. The shell of *C. fornicata* living inside the aperture is flatter than that of *Grandicrepidula grandis* living inside the aperture (H/L ratio of 0.30 ± 0.025 (n=18); Vermeij, 1989), but not as flat as that of *E. walshi* (H/W ratio of 0.11 to 0.18 or 0.14 ± 0.027 (n=6)). Also, it is elongate whereas *E. walshi* typically has a wide shell (compare Figures 11–15 with 17–18) as it has its head towards the adapical side of the aperture (own observations; this is why above H/W ratio is used for *E. walshi*).

Species with flat white shells have evolved multiple times within *Crepidula* and as eco-phenotypes within *Crepidula* species (Collin, 2019). Although in our case the flatness of the shells has a logical explanation, no specific cause has thus far been identified for these shells being much lighter colored than specimens on the outside. Interestingly, the flatness and pale coloring only applies to *C. fornicata* directly attached to the host shell. Specimens that settle on these to form a stack have a more convex shape and (slightly) darker color (Figures 5, 7, 8, 10–12). Two specimens on the photograph from Florida (mentioned above) form a stack, with the specimen on top being more convex.

Whereas Yoshikawa et al. (2018) found *E. walshi* not showing host specificity for particular species of hermit crabs or snail shells, in Zuid-Holland *C. fornicata* occurs with the hermit crab *Pagurus bernhardus* in shells of *E. catena*, which is probably opportunistic as in this area these are currently the only large hermit crab and most frequent large gastropod. No *E. catena* have been found with shells of *C. fornicata* only on the inside.

That leaves the question why *C. fornicata* started occupying the narrow space inside the aperture. Yoshikawa et al. (2018) state that for *E. walshi* this position gives protection from physical disturbances and predation. Water currents set up by the feeding of the hermit crab are beneficial to epibionts (Conover, 1979), from which calyptraeids inside the aperture will benefit more. Specifically for *C. fornicata* in Europe, competition with other epibionts of hermit crabs may be the main reason for choosing this position (competition between epibionts is discussed by Karlson and Shenk, 1983). Shells with *C. fornicata* on the inside typically have numerous *Crepidula fornicata* and other commensals (e.g. barnacles, Figures 5, 6, 10) on the outside (Table 2). No shells have been found with *C. fornicata* on the inside, but not on the outside. This is an indication that the inside is a less preferred place that most likely is chosen at a later stage, which would make sense as growth is greatly inhibited and the animal has to build more shell for a small increase in volume. The position on the adapical side of the aperture appears to rank below that on the inside, although a single shell was found with *Crepidula fornicata* on the outside and in this position, but none on the inside of the aperture (and no indication one has been present). In its native range, this competition likely plays a lesser role as large gastropod shells are plentiful (Conover, 1979). The shells themselves are also much larger (for example the *Sinistrofulgur sinistrum* mentioned above can be up to 45 cm long) and thus each shell occupied by a hermit crab provides space for many more epibionts than the *Euspira catena* shells of <4 cm long in the study area. Karlson and Shenk (1983) reported 96 *C. fornicata* from the outside of a single *Busycon carica* (Gmelin, 1791) shell.

The shells with numerous and/or large *Crepidula fornicata* may have been abandoned by the hermit crab that occupied them. Hermit crabs change shells as they grow and carefully select the shell to live in (own observations and Yoshikawa et al, 2018). The presence of symbionts influences shell selection, Conover (1976) describes how all

hermit crabs he studied rejected shells containing barnacles. Some rejected shells had *C. fornicata*, which, depending on their weight and position, may impact the center of gravity of the system. Shells with *C. fornicata* on the outside were more often tolerated than those with *C. fornicata* on the inside. On the other hand, the presence of hydroids positively influenced selection (Conover, 1976). The skeleton of hydroids often expands the total shell volume, allowing the crab to continue using it (own observations).

The geographic patterns of habitat generalists and specialists in calyptraeids are not yet properly understood (Vermeij, 1989; Collin, 2019). Only for part of the species (and therefore genera), their life habits as generalist or specialist have been documented. Very few photographs are available of calyptraeid shells inside the aperture of hermit crab occupied shells (e.g., Collin, 2019: fig. 1A). Such information is required as basis for a theoretical framework that can predict shifts as described in this paper, which could be caused by migration, changes in number of type of available shells, competition with other symbionts (including of the same species), etc. According to Low and Tan (2014) and Yoshikawa et al. (2018), *Ergaea walshi* is also found on other substrates, e.g. underneath horseshoe crabs or on dead bivalves. However, it is never found on the outside of gastropods, whether occupied by a hermit crab or not (own observations). The species of the *C. plana* complex can also be found on the outside and other substrates (Collin, 2000). In northwestern Borneo, shells occupied by hermit crabs frequently host another calyptraeid, *Desmaulus extinctorium* (Lamarck, 1822), which lives only on external shell surfaces and is never found on the inside or on another substratum (own observations).

The understanding of the behavior of calyptraeids as habitat generalist or specialist is also relevant for the recognition of hermit crab-occupied shells in the fossil record. Walker (1992) specifically mentions that external shell-inhabiting species of *Crepidula* are not good indicators of hermit crab occupancy, but *Crepidula* that inhabit gastropod apertures are excellent indicators. In the current study it was found that, specifically for *C. fornicata* shells with *C. fornicata* on the outside were likely, but not certainly inhabited by a hermit crab, as the species lives on various substrates. If a flat specimen of *C. fornicata* is present on the inside, it is likely that the shell has been inhabited by a hermit crab: *C. fornicata* will not limit its growth if there is no crab. Other indications

Table 1. Overview of *Euspira catena* found at the localities discussed.

	Scheveningen Jan. 2017	Hoek van Holland Jan. 2017	Hoek van Holland Feb. 2019
Number of *Euspira catena* alive	tens	tens	tens
Number of *Euspira catena* dead	hundreds	hundreds	hundreds
Number of *Euspira catena* with hermit crabs and *Crepidula fornicata* on outside	tens	tens	tens
Number of *Euspira catena* with hermit crabs and *Crepidula fornicata* inside and on outside	3	3	7

Table 2. Overview of all shells with *C. fornicata* on the inside. Note all shells directly attached to the host shell are assumed to be females.

| | | | Outside | | Inside | | Front | | |
	Locality	Date	Host shell	# females	Max. # of specimens in stack	# females	Max. # of specimens in stack	Specimen on upper left	Total # specimens	Remarks
1	Scheveningen	Jan. 2017	*Euspira catena*	2	3	1	2	1	7	Numerous barnacles, boring sponge
2	Scheveningen	Jan. 2017	*Euspira catena*	2	1	1	1	0	3	Barnacles
3	Scheveningen	Jan. 2017	*Euspira catena*	1	1	1	1	0	2	Numerous barnacles, boring sponge, bryozoans
4	Hoek van Holland	Jan. 2017	*Euspira catena*	1	3	1	4	0	7	No space left for host; barnacles, sea mat, boring sponge, bryozoans
5	Hoek van Holland	Jan. 2017	*Euspira catena*	2	1	1	2	0	4	On inside a female with two males. Barnacles, sea mat, boring sponge, bryozoans
6	Hoek van Holland	Jan. 2017	*Euspira catena*	0	0	1	2	0	2	Sea mat, boring sponge
7	Hoek van Holland	Mch. 2019	*Euspira catena*	2	2	1	1	0	4	Boring sponge, sea mat
8	Hoek van Holland	Mch. 2019	*Euspira catena*	1	4	1	1	0	5	Barnacles, sea mat
9	Hoek van Holland	Mch. 2019	*Euspira catena*	7	3	1	2	0	16	On outside one female with a stack and two other males; barnacles, sea mat
10	Hoek van Holland	Mch. 2019	*Euspira catena*	1	3	1	1	0	7	On outside one female with two stacks and another male; boring sponge, sea mat, barnacles, bryozoans
11	Hoek van Holland	Mch. 2019	*Euspira catena*	1	2	1	2	1	6	On outside one female with two males; barnacles, sea mat
12	Hoek van Holland	Mch. 2019	*Euspira catena*	2	?	1	2	0	4+	Specimens on outside fell off (two marks left); boring sponge, barnacles
13	Hoek van Holland	Mch. 2019	*Euspira catena*	4	?	2	1	0	6+	Inside has one small convex specimen attached individually. Specimens on outside fell off (four marks left)
14	*Hoek van Holland*	*Mch. 2019*	*Buccinum undatum*	2	2	1	3	1	7	No space left for host; slipper shells large, have been present long time; boring sponge, sea mat, barnacles and bryozoans.

Figures 11–18. Calyptraeidae. **11–15.** *Crepidula fornicata* found inside the aperture of hermit crab-inhabited *Euspira catena*, Scheveningen, Jan. 2017. **11–12.** Slipper stack (Table 2: 1). **11.** Female (L = 17.6 mm, H = 4.6 mm). **11a.** Ventral view. **11b.** Dorsal view. **11c.** Lateral view. Note the protruding septum. **12.** Male (L = 9.7 mm, H = 3.7 mm). **12a.** Lateral view, "stretched" to same length as female to show difference in shape and resulting space available. **12b.** Ventral view. **13.** Shell from *E. catena* in Figure 5 (Table 2: 3) (L 14.4 mm, H 3.3 mm. **13a.** Ventral view. **13b.** Dorsal view. **14.** Dorsal view (Table 2: 2) (L = 19.9 mm, H = 4.7 mm). **15.** Shell from *Euspira catena* in Figure 7 (Table 2: 4). Base of a stack of four (L = 26.0 mm, H = 5.5 mm). **15a.** Ventral view. **15b.** Dorsal view. **16.** *Euspira catena* (H = 32.6 mm) with imprints of *C. fornicata* on the outside, Hoek van Holland, Feb. 2019 (Table 2: 13). Note in this (rare) case not only the foot left an imprint, but also the tentacles and lips. The animals were oriented toward the aperture. This specimen also had a *Crepidula fornicata* inside the aperture. **17–18.** *Ergaea walshi* found inside the aperture of hermit-crab inhabited gastropods, Piasau Beach, Miri, Sarawak, Malaysia, June-Sept. 1992. **17.** Adult female (W = 33.2mm, H = 5.6 mm). Note the laterally elongate, concave shape (optimally conforming to the inside surface of the host shell), the septum indicating the thickness of the living specimen, the barnacle, and the imprint of another barnacle. **17a.** Ventral view. **17b.** Dorsal view. **17c.** Lateral view. Note the protruding septum. **18.** Juvenile male (W = 6.6 mm, H = 1.3 mm). Note rounded shape. **18a.** Ventral view. **18b.** Dorsal view.

that a shell has been inhabited by a hermit crab are specific wear-and-tear patterns and the presence of other symbionts: barnacles, sea mat, etc. (own observations; Walker, 1992 gives many examples). The recognition of shells that have been occupied by hermit crabs is relevant both for recent communities and fossil thanatocoenoses, as hermit crabs frequently displace shells to different depositional environments than those where the mollusks lived (own observations in northwestern Borneo and Walker, 1989). It would be useful to construct a broader framework including all calyptraeid species.

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The Miocene to Recent biogeographic history of vesicomyid bivalves in Japan, with two new records of the family

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ABSTRACT

We report on two fossil species of the chemosymbiotic bivalve family Vesicomyidae that were recently collected from Cenozoic strata in Japan. The new species *Pleurophopsis matsumotoi* is described from the upper Oligocene to lower Miocene Hioki Complex in Kochi Prefecture, and the extant species *Calyptogena pacifica* Dall, 1891 is reported from the upper Miocene Onnagawa Formation in Akita Prefecture. With these new records, vesicomyid bivalves in Japanese strata show the following distribution pattern through the latter half of the Cenozoic Era: during the early to middle Miocene *Pleurophopsis* was the dominant genus and is found in sediments of both the Japan Sea and the Pacific Ocean. From the late Miocene through to today *Archivesica* and *Calyptogena* are the most common genera. Of these, *Calyptogena* species including the extant *C. pacifica*, are the most common vesicomyids in the cold waters of the Japan Sea, whereas *Archivesica* species are mostly found in the warmer waters of the Pacific side of Japan. Since the late Miocene, the diversity of vesicomyids rapidly increased in the Japan Sea, probably because of the semi-enclosed geographic situation with opened northern straits.

Additional Keywords: *Pleurophopsis*, *Calyptogena*, fossil, paleobiogeography

INTRODUCTION

Vesicomyids are peculiar bivalves that derive their nutrition from symbiotic, sulfur-oxidizing bacteria (Fisher, 1990). They include the iconic Giant White Clam *"Calyptogena" magnifica* that was discovered at deep-sea hydrothermal vents in the late 1970s (Boss and Turner, 1980). To date, more than 100 extant species have been found at hydrothermal vents, hydrocarbon seeps, and whale falls (e.g., Taylor and Glover, 2010; Krylova et al., 2010). Vesicomyids also have a good fossil record, including more than 30 named fossil species, the oldest

being from the middle Eocene (Amano and Kiel, 2007; Kiel and Taviani, 2017; and references therein).

Japan has a rich Cenozoic fossil record of hydrocarbon seeps, whale falls, and organic-rich shales, from which species belonging to five vesicomyid genera have been reported: *Adulomya* Kuroda, 1931 (= *Pleurophopsis* Van Winkle, 1919, see discussion below), *Archivesica* Dall, 1908, *Calyptogena* Dall, 1891, *Hubertschenckia* Takeda, 1953, and *Pliocardia* Woodring, 1925 (Kanno et al., 1989; Amano and Kiel, 2007, 2010, 2011, 2012; Amano and Suzuki, 2010; Amano, 2014). Of these genera, *Hubertschenckia* is an exclusively fossil genus known from upper Eocene to lower Oligocene strata. Only two extant species are known from the fossil record: *Calyptogena pacifica* Dall, 1891 and *Archivesica kawamurai* (Kuroda, 1943) (Amano and Jenkins, 2011). Although numerous new vesicomyid species have been discovered and described in the last two decades, the history of this family in Japan has never been thoroughly reviewed from a biogeographic point of view.

Here we review and discuss the biogeographic history of vesicomyid bivalves in the Miocene–Recent of Japan, describe a new species of *Pleurophopsis* from the "Muroto Formation" in Kochi Prefecture, Shikoku, and report the new fossil record of *Calyptogena pacifica* from the Onnagawa Formation in Akita Prefecture, Honshu.

MATERIALS AND METHODS

We carried out a comprehensive review of the literature on fossil vesicomyids in Japan to assess their paleobiogeographic distribution, including the two records reported herein. Excluded from the review are the vesicomyids from the lower to middle Miocene Taishu Group (Ninomiya et al., 2014) in Tsushima Island at the western entrance of the Japan Sea. This is so because most specimens described by Ninomiya (2011) are deformed

and internal shell features were not illustrated, hence their generic assignments remain uncertain.

The four specimens described here as *Pleurophopsis matsumotoi* new species were collected from a limestone nodule from mudstone of the Hioki Complex of the Nabae Group. The nodule included also some specimens of a thyasirid bivalve of the genus *Conchocele*. It was found about 1,500 m north of Mitsu Maruyama, Muroto City, in Kochi Prefecture, Shikoku, Japan (at 33°18′15″ N, 134°11′23″ E; Figure 1, Loc. 1). The vesicomyid specimens were previously reported as "*Akebiconcha uchimuraensis*" by Matsumoto and Hirata (1972). The age of the Hioki Complex was considered as late Oligocene based on planktonic foraminifera (Taira et al., 1980) and as late Oligocene to early Miocene based on radiolarian fossils (Suyari et al., 1989).

Seven specimens identified as the extant species *Calyptogena pacifica* Dall were recovered from a calcareous concretion derived from shales of the Onnagawa Formation, found as float under the bridge at Ashigafuchi, Chokai-cho, Yurihonjo City in Akita Prefecture, Honshu, Japan (at 39°11′15″ N, 140°11′39.8″ E; Figure 1, Loc. 2). The age of the Onnagawa Formation around this locality is considered as late Miocene (around 8.4 Ma) based on radiolarian fossils (Tsuji et al., 1991).

All specimens described and illustrated here are deposited in National Museum of Nature and Science, Tsukuba, Japan (NMNS PM for fossils and NSMT-Mo for Recent specimens).

SYSTEMATICS

Family Vesicomyidae Dall and Simpson, 1901

Genus *Pleurophopsis* Van Winkle, 1919
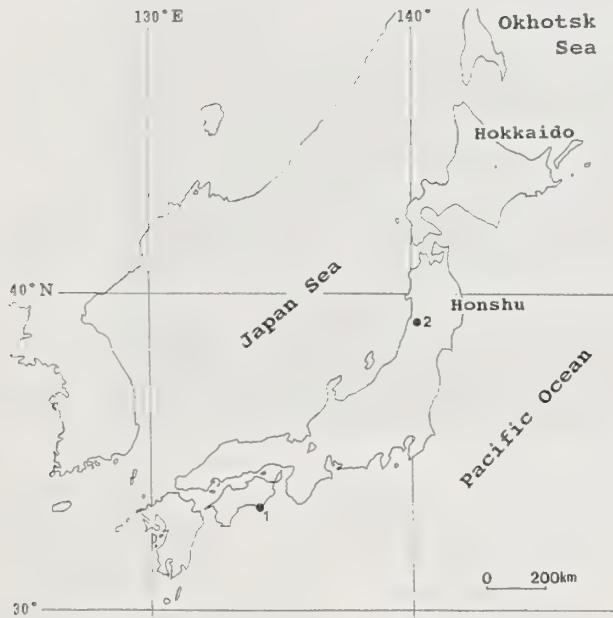
Figure 1. Localities of the new vesicomyid fossils described in this paper.

Type Species: *Pleurophopsis unioides* Van Winkle, 1919 (monotypy), middle Miocene, Trinidad (Van Winkle, 1919; Kiel, 2007).

Remarks: The genus *Pleurophopsis* was introduced and used for elongated, fossil vesicomyids from the Caribbean region, Peru and Ecuador (Van Winkle, 1919; Olsson 1931, 1942). Its shell characters are virtually identical to those of *Adulomya* Kuroda, 1931, including an elongate shell, two cardinal teeth in the right valve, the anterior original point of the pallial line at the posterior side of anterior adductor muscle scar, and the lack of a pallial sinus and a subumbonal pit (Kiel, 2007; Krylova et al., 2010). Kiel (2007) considered the genus doubtful because the type material of *Pleurophopsis unioides* is lost and the then available material lacked critical hinge features to fully characterize the species; he suggested using *Adulomya* instead. Krylova et al. (2010) essentially followed this view, but Krylova and Sahling (2010) included *Pleurophopsis* in their list of vesicomyid genera. Ongoing work on new material of *Pleurophopsis unioides* from the type locality (SK and CTS Little) indicates that *Pleurophopsis* is a valid genus and that *Adulomya* should be synonymized with it. The name *Adulomya* has long been used for elongated fossil vesicomyids in Japan (Kanno et al. 1998; Majima et al. 2005; Amano and Kiel, 2007, 2011; Isaji, 2013; Miyajima et al., 2017) and virtually all species previously assigned to *Adulomya* match the characteristics of *Pleurophopsis*. Only two species show a slight deviation: in *Adulomya chitanii* Kanehara, 1937, the pallial line bends backwards before reaching the posterior adductor scar; this is unlike other *Adulomya/Pleurophopsis* species but we consider this not to represent an actual pallial sinus. *Adulomya hokkaidoensis* Amano and Kiel, 2007 has a very small subumbonal pit, which, however, is very unlike the large and elongate-triangular subumbonal pit of *Ectenagena elongata* (Dall, 1916) which is otherwise very similar.

Abyssogena Krylova, Sahling, and Janssen, 2010 is an extant vesicomyid genus with very elongated shells. In particular, the deep-sea living species *Abyssogena phaseoliformis* (Métivier, Okutani, and Ohta, 1986) from the Japan, Kurile, and Aleutian Trenches, resembles the type species of *Adulomya*, *A. uchimuraensis* (Kuroda, 1931) in having a large and very elongated shell (Figure 9). However, as Krylova et al. (2010) observed, *Abyssogena* can be easily distinguished from *Pleurophopsis* in having an anterior original point of the pallial line located at ventral part of the anterior adductor muscle scar and possessing an indistinct and irregular shaped pallial sinus (Figures 8, 11, 12).

Like *Pleurophopsis* and *Abyssogena*, *Ectenagena* Woodring, 1938 also has an elongate shell and two cardinal teeth in the right valve. *Ectenagena* also shares with *Pleurophopsis* the anterior point of origin of the pallial line located at the posterior part of anterior adductor muscle scar (Krylova et al., 2010). However, *Ectenagena* has a small (up to 50 mm; Coan et al., 2000), very thin, compressed shell with a short nymph. Further, unlike *Abyssogena* and *Pleurophopsis*

Figures 2, 3, 5–7, 10, 11, 13, 14. *Pleurophopsis matsumotoi* new species. **2, 3.** Right-valve hinges, NMNS PM13233. **5.** Paratype (NMNS PM13227), left valve showing anterior adductor muscle scar (AAS) and anterior original point of pallial line (white arrow). **6, 11, 13.** Holotype (NMNS PM13228). **6.** Dorsal view. **11.** Left valve, showing anterior adductor muscle scar (AAM) and anterior original point of pallial line (white arrow). **13.** Right valve, showing posterior adductor muscle scar (PAS) and posteriorly backward bent pallial line (white arrow). **7.** Dorsal view, NMNS PM28254. **10.** Left valve, showing posterior adductor muscle scar (PAS) and posteriorly backward bent pallial line (white arrow), NMNS PM28255. **14.** Right valve, showing posterior adductor muscle scar (PAS) and posteriorly backward bent pallial line (white arrow), NMNS PM13256. **Figures 4, 9, 12.** *Pleurophopsis uchimuraensis* (Kuroda). **4.** Left valve hinge, NMNS PM28257. **9.** Left valve, NMNS PM28258. **12.** Right valve, showing anterior adductor muscle scar (AAS) and the original point of pallial line (white arrow), NMNS PM28259. **Figure 8.** *Abyssogena phaseoliformis* (Métivier, Okutani and Ohta), Holotype, NSMT-Mo 64164, showing anterior adductor muscle scar (AAS) and the original point of a pallial line (white arrow). Scar bars = 10 mm.

(except for *P. hokkaidoensis*), the hinge of *Ectenagena* has a deep subumbonal pit.

Pleurophopsis matsumotoi new species
(Figures 2, 3, 5–7, 10, 11, 13, 14)

Akebiconcha uchimuraensis (Kuroda). Matsumoto and Hirata, 1972: 755–757, pl. 1, figs. 1–8, pl. 2, figs.1–2.
Adulomya? sp. Amano and Kiel, 2011: figs. 30–31.

Diagnosis: A large-sized, well-inflated and moderately elongate *Pleurophopsis*; antero-dorsal margin short, posterior margin subtruncated, ventral margin concave; narrow hinge plate with thin anterior cardinal tooth (1) and rather thick posterior cardinal tooth (3b); posterior end of pallial line turning toward to anterior before reaching posterior adductor muscle scar.

Holotype: Internal mold of articulated specimen (NMNS PM 13228), length 112.5 mm, height 39.3 mm.

Paratype: Internal mold of articulated specimen (NMNS PM 13227), length 93.1 mm+, height 36.9 mm (from the type locality).

Type locality: 1.5 km north of Mitsu, Muroto City in Shikoku, Japan (Matsumoto and Hirata, 1972).

Material examined Four specimens from the type locality.

Description: Shell up to 112.5 mm long, elongate (height/length-ratio = 0.34), equivalve and inequilateral, well inflated (width/height-ratio = 0.67–0.73). Surface sculptured only by rough, irregular growth lines. Beak situated anteriorly at about one-fifth of shell length. Antero-dorsal margin short and nearly straight, graduating into rounded anterior margin; ventral margin concave; postero-dorsal margin straight, gently sloping, posterior margin subtruncated. Escutcheon and lunule absent. Hinge plate narrow, with two cardinal teeth in right valve; anterior cardinal tooth (1) very thin and inclined anteriorly; posterior cardinal tooth (3b) rather thick and oblique posteriorly; no subumbonal pit. Ligament occupying two-fifth of the postero-dorsal margin. Anterior adductor muscle scar ovate, bordered posteriorly by thick ridge; posterior adductor muscle scar ovate, less distinct than the anterior scar; distinct ridge running from umbonal area to ventral side of posterior muscle scar. Original point of pallial line located at posterior part of anterior adductor muscle scar, and pallial line at posterior end bent toward to anterior before reaching posterior adductor muscle scar.

Remarks: *Pleurophopsis matsumotoi* new species represents the as-yet oldest record of *Pleurophopsis* (= *Adulomya*) in Japan.

Comparison: *Pleurophopsis matsumotoi* differs from *P. uchimuraensis* (Kuroda) (Figure 4, 9, 12) in having a much more higher shell (height/length-ratio = 0.34 compared to 0.17–0.24 in *P. uchimuraesnis*; Kanno

et al., 1998, Amano and Kiel, 2011), an inflated concave ventral margin, and the pallial line turning backward before reaching the posterior adductor muscle scar. *Pleurophopsis matsumotoi* also shares the posteriorly backward bent pallial line with *P. chitanii* (Kuroda). However, *P. matsumotoi* has a larger shell than *P. chitanii* (up to 70.4 mm in length) and a concave ventral margin. The present new species differs from other *Pleurophosis* such as *P. akanudaensis* (Tanaka), *P. hamuroi* Amano and Kiel, *P. kuroiwaensis* Amano and Kiel from Japan in having larger, more inflated shell and a concave ventral margin.

Distribution: Only from the type locality.

Etymology: For Dr. Eiji Matsumoto who collected the type material of this new species.

Genus *Calyptogena* Dall, 1891

Type Species: *Calyptogena pacifica* (Dall) (monotypy), Recent, southeastern Alaska.

Calyptogena pacifica Dall, 1891
(Figures 15–24, Table 1)

Calyptogena pacifica Dall, 1891: 190; Dall, 1895: 713, pl. 25, fig.4; Grant and Gale, 1931: 278–279, pl. 13, fig. 13a, b; Otuka, 1937: text-fig.; Woodring, 1938: fig. 2b; Otatume, 1942: 435–437, pl.16, figs.1–12; Okutani, 1966: 301, pl.27, figs. 1, 3; Boss, 1968: figs.16, 17, 19, 20; Keen, 1969: N664, fig. E138, 11a, b; Tiba, 1972: 155, pl. 19, figs.6, 6a; Amano and Kanno, 1991: figs. 4.18, 4.19; Horikoshi and Hashimoto, 1992: pl. 1, fig. 4a, pl. 2, fig. 4b; Okutani et al., 1993: fig. 7; Okutani, 2000: 997, pl. 496, fig. 7; Amano, 2002: 27, figs. 3.4, 3.9; Amano, 2003: figs. 3–14; Amano and Kanno, 2005: 204–207, fig. 3; Krylova and Sahling, 2006: 362–368, figs. 3–6; Suzuki, 2007: figs. III-3-4.5, III-3-4.6; Huber, 2010: 354; Amano and Jenkins, 2011: 166–169, figs. 3–16; Nevesskaja et al., 2013: fig. 150-9; Okutani, 2017: 1233, pl. 528, fig. 8.
Unio moraiensis Suzuki, 1941: 55–56, pl. 4, figs. 2–5.
Calyptogena (Calyptogena) pacifica Dall. Bernard, 1974: 11, figs.1A, 2A, 3A, 4A–D; Boss and Turner, 1980: 188–189, figs.10B, C; Kanno et al., 1989: figs. 1.7–1.15.
?*Calyptogena* sp. Tsuji et al., 1991: fig. 25, 26.
Vesicomya (Calyptogena) pacifica (Dall). Coan et al., 2000: 341, pl. 70.

Material Examined: Seven specimens. NMNS PM28260–PM28266.

Remarks: The shells are rather small (less than 30.0 mm in length) and ovate in outline (height/length = 0.68, 0.71). Their beaks are located at anterior one-fifth to two-fifths of shell length (umbo% = 21, 41). In the right valve, a posterior tooth (3b) is large and triangular with a small thin anterior tooth (3a), showing U-shaped connection, and surrounding a small middle tooth (1). The pallial line is entire. These shell and hinge characters are identical to
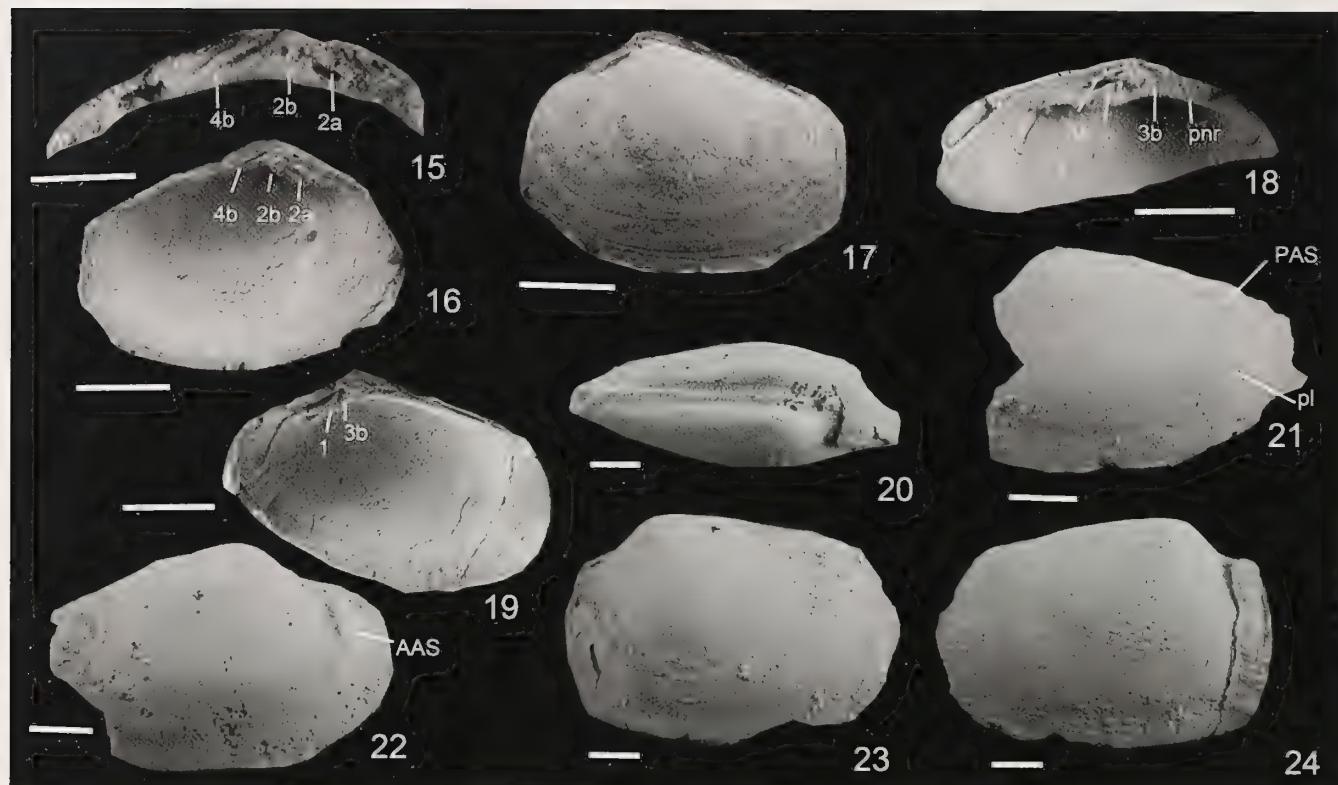
Figures 15–24. *Calyptogena pacifica* Dall from the upper Miocene Onnagawa Formation. **15.** Left valve hinge, silicone rubber cast, NMNS PM28263. **16, 17, 19. 16.** Silicone rubber cast of inner part of left valve. **17.** Left valve. **19.** Silicone rubber cast of inner part of right valve; NMNS PM28260. **18.** Rubber cast of right valve hinge, NMNS PM28261. **20, 23, 24. 20.** Dorsal view. **23.** Left valve. **24.** Right valve; NMNS PM28262. **21.** Inner part of left valve, showing pallial line (pl) and posterior adductor muscle scar (PAS), NMNS PM28264. **22.** Inner part of right valve, showing anterior adductor muscle scar (AAS), NMNS PM28265. Scar bars in 15–19 = 5 mm and 20–24 = 10 mm.

those of Recent *Calyptogena pacifica* specimens. Tsuji et al. (1991: fig. 25, 26) identified and illustrated a specimen as *Calyptogena* sp. collected from the Onnagawa Formation, near the fossil locality discussed here. Although no pallial line and hinge features were shown, the outline of their specimen is similar to that of *Calyptogena pacifica* illustrated here. (See Table 1 for morphometric data.)

Comparison: The oldest species of *Calyptogena*, *C. katallaensis* Kiel and Amano, 2010 from the Oligocene Kulthieth Formation in Alaska is most similar to *C. pacifica*. However, *C. pacifica* differs slightly from the Oligocene species by having a nymph with a rather abrupt

end and a long anterior cardinal tooth (3a) in the right valve.

Distribution: Upper Miocene: Morai Formation (Otatume, 1942; Amano, 2003) and Toyama Formation (Suzuki, 2007) from Hokkaido, Akaishi Formation (Amano and Jenkins, 2011) from Aomori Prefecture, Onnagawa Formation (this study) from Akita Prefecture, Nodani Formation (Kanno et al., 1989; Amano, 2002) from Niigata Prefecture; Pliocene: Kurokura, Kawazume and Nadachi Formations (Kanno et al., 1989; Amano and Kanno, 1991; Amano and Kanno, 2005) from Niigata Prefecture; middle Pleistocene: Wakimoto Formation (Otuka, 1937) from Akita Prefecture; Recent: Sea of

Table 1. Morphometry of *Calyptogena pacifica* studied.

Measurements (mm):	length (L)	height (H)	H/L	Umbo (%)*	Valve
NMNS PM28260	18.0	12.3	0.68	41	left
NMNS PM28262	30.0	21.3	0.71	21	left
NMNS PM28263	29.6	+18.9	-	-	left

* Ratio of anterior length (distance from umbo to anterior margin) to shell length.

Okhotsk (Tiba, 1972), Dixon Strait, Alaska to Monterey Bay, California (Coan et al., 2000).

BIOGEOGRAPHIC DISTRIBUTIONS OF MIOCENE TO RECENT VESICOMYIDS IN JAPAN

In this section, we review the geographic distribution of vesicomyid species and genera in Japan from the Miocene to the present (Table 2) in relation to tectonics, paleogeography, and climate. Following the appearance of *Pleurophopsis matsumotoi* new species around the early Miocene, *Pleurophopsis* was the dominant vesicomyid genus in Japan until the middle Miocene. The Japan Sea was formed in the early Miocene and, initially, had deep-water connections with the Pacific Ocean through the central part of Honshu, an area called the Fossa Magna Region (Iijima and Tada, 1990; Ogasawara, 1994). The first vesicomyids to colonize the Japan Sea were *Pleurophopsis chitanii* and *Pliocardia kawadai*, with the oldest record from the lower Miocene Kurosedani Formation in Toyama Prefecture (Amano et al., 2019). Through the early Miocene to early middle Miocene, *Pleurophopsis chitanii*, along with *Pleurophopsis uchimuraensis* and *Pliocardia kawadai*, occurred both in the Japan Sea and the Pacific side of Japan, while a remarkable number of endemic species evolved in the Japan Sea, namely

Table 2. Age and distribution of the fossil vesicomyids without the Paleogene species in Japan. * Species from the Sea of Okhotsk. ** Bessho Formation in Nagano Prefecture is treated as the Japan Sea side.

Species	Age	Pacific	Japan Sea	Formation
Archivesica sp.	Pliocene	+		Horinouchi F.
Archivesica ? bosoensis (Kanie and Kuramoch, 2001)	Pliocene	+		Shiramazu F.
Archivesica shikamai Amano and Kiel, 2010	Pliocene	+		Ikego F.
Archivesica kawamurai (Kuroda, 1943)	Pliocene–early Pleistoscene	+		Tomioka F., Hitachi F., Na-arai F., Kurotaki F., Ikego F., Imaizumi F., Hijikata F., Tamari Siltstone, Shinzato F.
Archivesica kannoi Amano and Kiel, 2010	early Pliocene		+	Kurokura F.
Calyptogena veneriformis Amano and Kiel, 2012	early Pliocene		+	Kurokura F.
Pleurophopsis sp.	early Pliocene		+	Kurokura F.
Archivesica shiretokensis (Uozumi, 1967)*	late Miocene			Rusha F.
Archivesica nipponica (Oinomikado and Kanehara, 1938)	late Miocene–early Pliocene		+	Kubiki F., Araya F.
Calyptogena pacifica Dall, 1891	late Miocene–middle Pleistocene		+	Onnagawa F., Morai F., Toyama F., Akaishi F., Nodani F., Kawazume F., Nadachi F., Kurokura F., Wakimoto F.
Pleurophopsis kuroiwaensis (Amano and Kiel, 2011)	latest middle Miocene		+	Ogaya F.
Pleurophopsis akanudaensis (Tanaka, 1959)	middle Miocene		+	Bessho F.**
Pliocardia ? tanakai Miyajima, Nobuhara and Koike, 2017	middle Miocene		+	Bessho F.**
Pleurophopsis hokkaidoensis (Amano and Kiel, 2007)	early middle Miocene		+	Chikubetsu F.
Pleurophopsis hamuroi (Amano and Kiel, 2011)	early–early middle Miocene		+	Higashibessho F.
Pliocardia kawadai (Aoki, 1954)	early–middle Miocene	+	+	Honya F., Kurosedani F., Higashibessho F., Nupinai F.
Pleurophopsis uchimuraensis (Kuroda, 1931)	early–middle Miocene	+	+	Bessho F.**, Takinoue F., Shikiya F.
Pleurophopsis chitanii (Kanehara, 1937)	early–middle Miocene	+	+	Mizunoya F., Kamenoo F., Taira F., Morozaki G., Nupinai F., Kurosedani F.
Pleurophosis sp.	middle Miocene	+		Aokiyama F.
Archivesica sakoi Amano, Jenkins, Ohara and Kiel, 2014	early Miocene	+		Shikiya F.
Pleurophopsis matsumotoi n. sp	late Oligocene–early Miocene	+		Hioki Complex

Pleurophopsis hamuroi, *P. hokkaidoensis*, *P. akanudaensis*, and *P. kuroiwaensis* (Table 2).

The vesicomyid faunas both sides of Japan became more distinct from the late Miocene onward, when *Archivesica* and *Calyptogena* became the dominant vesicomyid genera. Several species of *Archivesica* have been documented from the Japan Sea and the Pacific side of Japan, but none of those species occurs on both sides of Japan (Table 2). However, there is no late Miocene record of *Archivesica* in Japan, partly because the late Miocene on the Pacific side is characterized by strata barren of molluscan fossils in northeastern Japan and by a hiatus in southwestern Japan (Chinzei, 1986). Fossils of *Calyptogena* are only known from the Japan Sea, including the extant *C. pacifica*. Remarkably, the timing of the faunal change from the dominance of *Pleurophopsis* to that of *Archivesica/Calyptogena* coincides with the tectonic inversion from tension to compression in Northeast Japan (Sato, 1994). However, potential reasons for this coincidence remain unclear. Vesicomyids became locally extinct in the Japan Sea due to deep-water anoxia during the Pleistocene glacial period; their absence from the present-day Japan Sea might be because they have been unable to pass through the shallow straits from the Pacific Ocean (Amano, 2001, 2007; Amano and Jenkins, 2011).

Based on the areas of origin and the ecology of the two extant vesicomyid species that have fossil records in Japan (*Calyptogena pacifica* Dall and *Archivesica kawamurai*; Amano and Jenkins, 2011), and their relatives, we postulate that the observed paleobiogeographic patterns might be broadly related to temperature preferences among *Calyptogena* and *Archivesica*. Present-day *Calyptogena pacifica* occurs mainly in the cold waters of the North Pacific Ocean (Coan et al. 2000). The genus *Calyptogena* first appeared in the Oligocene of Alaska (Kiel and Amano, 2010) and migrated southward to the Japan Sea in the late Miocene, potentially related to the late Miocene climate cooling (Amano and Jenkins, 2011). The Japan Sea at that time was connected to the Pacific Ocean mainly through its northern straits (Iijima and Tada, 1990; Ogasawara, 1994), and was probably blocked from influx of warmer waters from the south, thus providing a suitable habitat for *Calyptogena* species.

The oldest species of *Archivesica*, *A. sakoi* Amano, Jenkins, Ohara, and Kiel, 2014, is from the lower Miocene Shikiya Formation in Wakayama Prefecture on the Pacific side of southern Japan. From the late Miocene onward *Archivesica* also occurs in the Japan Sea, but during the same time it is more diverse and more widely distributed on the Pacific side, with extant *Archivesica kawamurai* and three further *Archivesica* species distributed from central Honshu to southwestern Japan (Amano and Jenkins, 2011; Table 2). The Pacific side of central Honshu to southwestern Japan has been influenced by warm-water currents since early Miocene (Ogasawara, 1994) and has been situated at a subduction zone, resulting in constant methane seepage (Amano and Jenkins, 2011). Today, *Archivesica* includes at least ten species living in the warm-water area from central Honshu to southwestern Japan on the Pacific side (Okutani, 2017) and is the most diversified genus among the vesicomyids.

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Two warm-water species of Trochoidea (Gastropoda) from Pliocene deposits on the Japan Sea side of Honshu, Japan, with remarks on the influence of the onset of Northern Hemisphere glaciation

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ABSTRACT

Two warm-water trochoidean gastropods are studied. One of them, *Monodonta joetsuensis* new species, is the first Pliocene record of this genus in Japan. Another, *Pomaulax omorii* (Shibata, 1957), is distributed widely along the Japan Sea side of Honshu. In the Japan Sea borderland, both species are confined to late Pliocene deposits and became extinct as a result of cooling at the onset of Northern Hemisphere glaciation near the end of the Pliocene (2.75 Ma). It has become clear that thirteen shallow-water suspension-feeding bivalves, including Miocene relict forms, and eleven grazing or predatory/scavenging gastropods that mostly lived in warm shallow-water disappeared from the Japan Sea during this cooling event.

INTRODUCTION

Many species of trochoidean gastropods live on rocky bottoms (Hickman and McLean, 1990). Fossils of these species are not plentiful, and are usually collected from sandy sediments or turbidites, deeper than their original living habitats. Two extinct species of Trochoidea have been recovered from the upper Pliocene desposits on the Japan Sea side of Honshu. One of them, a small trochid gastropod, is a new species of *Monodonta*, and the other, is a large turbinid gastropod *Pomaulax omorii* (Shibata, 1957). *Pomaulax omorii* was originally described by Shibata (1957) as *Astraea* (*Pachypoma*) *omorii* from the lower Pliocene Ochiai Formation in Kanagawa Prefecture, on the Pacific side of Honshu. On the Japan Sea side of Honshu, this species was illustrated as *Astralium* (*Distellifer*) aff. *rhodostoma* (Lamarck, 1822) by Amano et al. (2000b) from the upper Pliocene Tentokuji Formation. Fortunately, I collected some well-preserved specimens of *Pomaulax omorii* from the upper Pliocene formations in Niigata.

I describe the new species of *Monodonta*, redescribe the features of *Pomaulax omorii* from the Japan Sea borderland and discuss their paleogeographic significance.

Accordingly, I also discuss the influence of the onset of major Northern Hemisphere glaciation to the molluscan fauna in the Japan Sea borderland.

MATERIALS AND METHODS

Monodonta joetsuensis new species was recovered from an alternation of fine-graind sandstone, yielding pebbles and plant fragments, and dark gray mudstone of the Nadachi Formation, 220 m upstream from a tributary 0.8 km upstream from the Fujikake-dani River in Joetsu City, Niigata Prefecture (Figure 1, Loc. 4). From this locality, 18 species of gastropods and 22 bivalves co-occurred, crowded together (Table 1). Many shallow-water species were carried into deep water by turbidity currents—most bivalves, even the deep-sea bivalve *Calyptogena pacifica* Dall, 1891 are disarticulated at this site. Two warm-water species, *Thais clavigera* (Küster, 1860) and *Veremolpa micra* (Pilsbry, 1904), are associated with many cold-water or endemic extinct species. Calcareous nannofossils from this locality were identified by Tokiyuki Sato (Akita University), who indicated that their ages fall within the lower to middle part of zone NN16 (Martini, 1971; 3.66–2.75 Ma).

Seventeen specimens of *Pomaulax omorii* were obtained from pebble-bearing sandstones of the lower part of the Tentokuji Formation at the large cliff along the Sannai River in Kami-Sannai, Akita City, Akita Prefecture (Figure 1, Loc. 1). This locality corresponds to the fossil locality described by Shimamoto and Koike (1986) and the Loc. 2 of Amano et al. (2000b). The age of the Tentokuji Formation was assigned to the lower to middle zone NN16 (3.85–2.75Ma) via calcareous nannofossils (Amano et al., 2000). Some warm-water species such as *Erronea* sp. and *Oliva mustelina* Lamarck, 1811 were collected with many cold-water mollusks (Amano et al., 2000b; Table 2). One specimen of *Pomaulax omorii* was also collected from a calcareous concretion yielding plant debris included in siltstone of the upper part of the Araya

Figure 1. Localities of fossils.

Formation on the bank of the Maekawa River, 600 m south of Kiyamazawa, Nagaoka City, Niigata Prefecture (Figure 1, Loc. 2). The age of the upper part of this formation was assigned to the late Pliocene based on foraminifers by Kobayashi et al. (1991). Other than *Nemocardium samarangae* (Makiyama, 1934), the associated fauna consists of cold-water or extinct endemic species (Table 1). One more well-preserved specimen of *Pomalulax omorii* was collected from sandy siltstone of the Shitoka Formation, 550m upstream in the Shitoka River in Minami Uonuma City, Niigata Prefecture (Figure 1, Loc. 3). The age of the Shitoka Formation was assigned to the late Pliocene based on calcareous nannofossils by Amano et al. (2009). Many cold-water species and one warm-water species, *Nemocardium samarangae* (Makiyama, 1934), are associated with this specimen (Table 2).

I have followed the arrangement in Bouchet et al. (2017). All pictures were taken with the specimens covered with ammonium chloride. All specimens are deposited at the National Museum of Nature and Science, Tsukuba (NMNS PM).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Subclass Vetigastropoda Salvini-Plawen, 1980
Order Trochida Cox and Knight, 1960
Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Monodontinae Gray, 1857

Genus *Monodonta* Lamarck, 1799

Type Species: *Trochus labio* Linnaeus, 1758 by monotypy.

Remarks: According to Williams et al. (2010), the subfamily Monodontinae includes three genera: *Monodonta* Lamarck, 1799, *Austrocochlea* P. Fischer, 1885 and *Diloma* Philippi, 1845. Based on molecular and morphological data, *Austrocochlea* seems to be very close to *Monodonta* (Donald et al., 2005; Willams et al., 2010). However, *Austrocochlea* has narrower spiral cords without any axial grooves, a weak tooth on the inner lip, and very weak crenulations inside the outer lip. *Diloma* differs from *Monodonta* in having no tooth on the inner lip and no crenulations inside the rather thin outer lip.

Monodonta joetsuensis new species
(Figures 2–5)

Diagnosis: Small *Monodonta* with 4.25 whorls and rather low spire, sculpture of about 20 spiral cords on last whorl, separated by nearly equal interspaces. Inner lip with prominent basal tooth and eight denticles inside outer lip.

Description: Shell small (9.5 mm in height, 10.4 mm in diameter), rather thick, turbiniform with relatively low spire; protoconch decolated; teleoconch with 4.25 whorls; suture deep. Surface sculptured with growth lines and spiral cords; growth lines distinct, particularly near aperture, and oblique posteriorly; spiral cords separated by nearly equal interspaces, seven on penultimate whorl, twenty on last whorl, cords color alternating light and dark gray; area below substural wide cord concave, sculptured with three fine cords. Aperture circular; columella arched, with prominent basal tooth, deeply notched below; interior of outer lip crenulated by eight denticles.

Holotype: NMNS PM 28267 (9.5 mm in height, 10.4 mm in diameter).
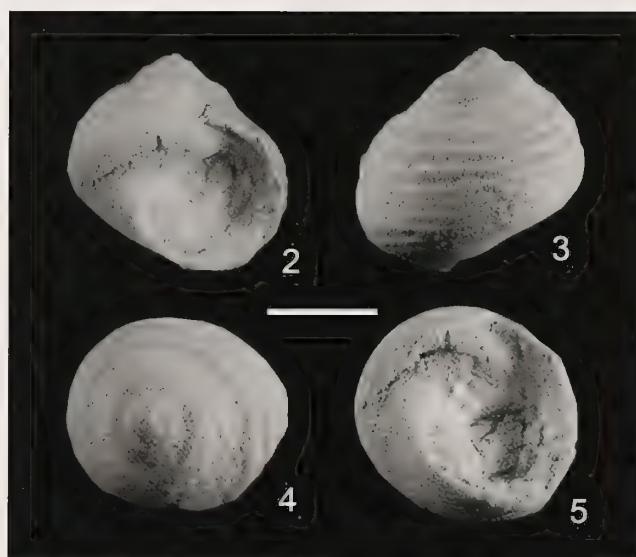
Figures 2–5. *Monodonta joetsuensis* new species, **holotype,** NMNS PM 28267) from the Nadachi Formation. **2.** Apertural view. **3.** Abapertural view. **4.** Apical view. **5.** Basal view. Scale bar = 5 mm.

Table 1. Molluscan fossils associated with *Monodonta joetsuensis* new species from the upper Pliocene Nadachi Formation (Loc. 4 in Figure 1). * warm-water species.

Species
Notoacmaea sp.
Cocculina japonica Dall
Homalopoma noctrum (Gould)
Monodonta joetsuensis new species
Umbinium (*Suchium*) *akitanum* Suzuki
Omphalius aff. *rusticus* (Gmelin)
Bittium sp.
Littorina brevicula (Philippi)
Turritella (*Naohaustator*) *saishuensis motidukii* Otuka
Euspira pallida (Broderip and Sowerby I)
Neverita (*Glosaulax*) *vesicalis* (Philippi)*
Cryptonatica clausa (Boroderip and Sowerby I)
C. janthostoma (Deshayes)
Thais clavigera (Küster)*
Lirabuccinum fuscolabiatum (Smith)
Buccinum sp.
Mitrella bicincta (Gould)
Reticunassa acutidentata (Smith)
Acila (*Truncacila*) *nakazimai* Otuka
Leionucula niponica (Smith)
Portlandia (*Portlandella*) *toyamaensis* (Kuroda)
Nuculana (*Nuculana*) *onoyamai* Otuka
Anadara (*Scapharca*) *ommaensis* Otuka
Porterius dalli (Smith)
Glycymeris (*Glycymeris*) *yessoensis* (Sowerby III)
Chlamys (*Chlamys*) *cosibensis* (Yokoyama)
Anomia chinensis (Philippi)
Felaniella usta (Gould)
Astarte hakodatensis Yokoyama
Tridonta borealis (Schumacher)
"*Dinocardium*" *angustum* (Yokoyama)
Macoma (*Macoma*) *calcarea* (Gmelin)
Calyptogena pacifica Dall
Pseudamiantis tauyensis (Conrad)
Humilaria perlaminosa (Conrad)
Securella sp.
Veremolpa micra (Pilsbry)*
Protothaca tateiwai (Makiyama)
Anisocorbula venusta Gould
Myadora fluctuosa Gould

Type Locality: Small outcrop at 220 m upstream from a tributary 0.8 km upstream from the Fujikake-dani River in Joetsu City, Niigata Prefecture, Japan.

Remarks: This new species can be safely assigned to *Monodonta*, not to *Austrocochlea* nor *Diloma*, because it has a strong basal tooth and strong denticles inside the outer lip. The present species is most similar to the recent *Monodonta australis* Lamarck, 1822, from around the Ogasawara Islands, Okinawa Islands, Mariana Islands, Hawaii, and Australia (Higo et al., 1999) in having a similar number of cords (6–12 on the penultimate whorl and 15–22 on the last whorl) and a similar number of crenulations inside the outer lip (6–13). *Monodonta joetsuensis* new species, however, has narrow spiral cords, as in some species of *Austrocochlea*. In contrast, *M. australis* has flat spiral cords separated by deep grooves and crossed by vertical grooves near the aperture.

Another recent species, *Monodonta canalifera* Lamarck, 1822, differs from the present species in having fewer (14–18), lower spiral cords.

Etymology: Named after the city name of locality.

Distribution: Late Pliocene, Nadachi Formation in Niigata Prefecture.

Family Turbinidae Rafinesque, 1815
Subfamily Turbininae Rafinesque, 1815

Genus *Pomaulax* Gray, 1850

Type Species: *Trochus japonicus* Dunker, 1844 by subsequent designation.

Remarks: *Astraea* Röding, 1798 previously encompassed species now included in distinct genera such as *Astralium* Link, 1807, *Lithopoma* Gray, 1850, *Megastraea* MacLean, 1970, *Pomaulax* Gray, 1850, and others (see Alf and Kreipl, 2011). This usage is now considered outdated because many paraphyletic clades were included (based on molecular data by Williams (2007, 2012) and Williams et al. (2008)). The type species, *Astraea heliotropium* (Martyn, 1784) is the only living species left in this genus. It is restricted to New Zealand. *Astraea* can easily be distinguished from *Pomaulax* by presence of well-inflated whorls, a very wide umbilicus and many prominent, wide spines at the periphery. *Pachypoma* was established by Gray (1850), based on *Trochus caelatus* Gmelin, 1791 (see Bouchet, 2011). Thus, *Pachypoma* is a junior synonym of *Lithopoma*.

Megastraea, based on *Astraea undosa* (Wood, 1828), most closely resembles *Pomaulax*. *Megastraea* differs from *Pomaulax* by having an operculum with three spiny ridges, and one or two wavy spiral ridges on and above the periphery (see also Alf and Kreipl, 2011). However, recent molecular work shows a close relationship between *Pomaulax* and *Megastraea* (Willams, 2007: 2012).

Lithopoma, from the western Atlantic, is another genus similar to *Pomaulax*. *Lithopoma* can be discriminated from *Pomaulax* in generally having a smaller shell and a periphery with strong axial ridges or with hollow spines (see also Alf and Kreipl, 2011). Molecular data shows a close relationship with *Lithopoma* and *Pomaulax* (Willams, 2007, 2012).

Pomaulax omorii (Shibata, 1957)
(Figures 6–13, 15, 17)

Astraea (*Pachypoma*) *omorii* Shibata, 1957, p. 24, pl. 4, figs. 2a–c.
? *Omphalius pfeifferi* cf. *carpenteri* (Dunker), Ogasawara et al., 1986, pl. 26, figs. 7a–c.
Astralium (*Distellifer*) aff. *rhodostoma* (Lamarck), Amano et al., 2000b, pl. 1, figs.17a, b.
Astraea omorii Shibata, Matsushima et al., 2003, pl. 4, fig. 1, 2; Shiba et al., 2013, figs. 4.3, 4.4.
?non *Pomaulax omorii* (Shibata), Amano et al., 2011, figs. 5.13, 5.14.

Table 2. Molluscan fossils associated with *Pomaulax omorii* (Shibata) from Loc. 1 (Tentokuji Formation), 2 (Araya Formation), 3 (Shitoka Formation) in Figure 1. * warm-water species.

Species name Loc.	1	2	3
Puncturella nobilis A. Adams	+		
Lepeta cf. *lima* Dall	+		
Niveotectura pallida (Gould)	+		
Minolia sp.	+		
Turcica sp.	+		
Littorina sp.	+		
Turritella (Neohaustator) saishuensis saishuensis Yokoyama	+	+	
T. (N.) nipponica (Yokoyama)		+	
Erronea sp.*	+		
Neverita (Glossaulax) cf. *vesicalis* (Philippi)	+		
Cryptonatica janthostomoides (Kuroda and Habe)	+		
C. sp.			+
Fusitriton izumozakiensis Amano	+	+	
F. aff. *oregonensis* (Redfield)			+
Mohnia yanamii (Yokoyama)		+	
Neptunea (Neptunea) eos (Kuroda)	+		
N. (N.) insularis (Dall)		+	
N. sp.			+
Buccinum cf. *unuscarinatum* Tiba		+	
B. sp.	+		+
Oliva mustelina Lamarck*	+		
Fulgoraria prevostiana (Crosse)	+		
F. masudae Hayasaka			+
Propebela sp.			+
Antiplanes contraria (Yokoyama)		+	
Rectiplanes sanctiioannis (Smith)		+	+
Conidae gen. et sp. indet.*	+		
Acila (Acila) divaricata (Hinds)	+		
A. (Truncacila) insignis (Gould)	+	+	
A. (T.) aff. *castrensis* (Hinds)	+		
Leionucula cf. *niponica* (Smith)	+		
Malletia inermis Yokoyama	+		
Nuculana (Nuculana) pernula (Müller)			+
Yoldia (Cnesterium) notabilis Yokoyama			+
Y. sp.	+		
Portlandia (Portlandella) japonica (Adams and Reeve)	+		
P. (P.) toyamaensis (Kuroda)			+
Arca boucardi Jousseaume	+		
Anadara (Anadara) amicula (Yokoyama)	+		
Porterius dalli (Smith)	+		
Glycymeris (Glycymeris) albolineata (Lischke)	+		
G. (G.) nipponica (Yokoyama)	+	+	
Limopsis tajimae Sowerby	+		
L. cf. *tajimae* Sowerby	+		
L. oblonga (A. Adams)		+	
Musculus laevigatus (Gray)	+		
Megacrenella columbiana (Dall)		+	
Chlamys (Chlamys) cosibensis (Yokoyama)	+		
C. (C.) tamurae Masuda and Sawada	+		
Mizuhopecten yokoyamae (Masuda)	+		
M. sp.	+		

(Continued)

Table 2. (Continued)

| Species name Loc.	1	2	3
Yabepecten tokunagai (Yokoyama)	+		
Cycladicama cumingii (Hanley)*	+		
Felaniella usta (Gould)	+		
Cardita leana Dunker	+		
C. cf. *leana* Dunker	+		
Megacardita sp.	+		
Cyclocardia myogadaniensis (Itoigawa)	+		
Tridonta borealis Schumacher	+		
Nemocardium samarangae (Makiyama)*	+	+	+
Clinocardium (Ciliatocardium) ciliatum (Fabricius)	+		
Serripes groenlandicus (Bruguière)		+	
Spisula (Mactromeris) voyi Gabb	+		
S. (M.) grayana (Schrenck)	+		
Cadella lubrica (Gould)	+		
Macoma (Macoma) calcarea (Gmelin)	+	+	+
M. (M.) nipponica (Tokunaga)	+		
Securella cf. *stimpsoni* (Gould)	+		
S. chitaniana (Yokoyama)	+		
Phacosoma tomikawensis (Takagi)	+		
Pseudamiantis cf. *tauyensis* (Yokoyama)	+		
Pandora wardiana (A. Adams)			+
Entodesma naviculoides Yokoyama	+		

Type Locality: Bank of Hayato River near Ochiai, Kiyokawa Village, Kanagawa Prefecture: Ochiai Formation, Pacific side of central Honshu, Japan.

Original Description: "Shell trochoid, depressed, large, conic-pyramidal, solid, thick, broader than high: surface of whorls flat, declined, sculptured by oblique axial plicae, the plicae weaker on the upper but stronger on the lower where they become somewhat crossed: peripheral margin angulated: on the lower surface sculptured by nine spiral cords, with alternating weak knotted and smooth cords: the columella base somewhat elevated, umbilical area somewhat concave: aperture squarely rounded in outline, outer lip sharply inclined, basal lip thin: columella somewhat concave, smooth, tooth-like swelling on lower part." (Shibata, 1957, p. 24).

Material Examined: Two well-preserved specimens (NMNS PM 28268, 28269) from the Tentokuji Formation, one specimen (NMNS PM 28270) from the Araya Formation, and one well-preserved specimen (NMNS PM 28271) from the Shitoka Formation are examined.

Description of the Specimens from the Japan Sea Side of Honshu: Shell medium in size, attaining 51.8 mm+ in height, 56.8 mm in diameter, rather thick, trochiform with high spire; protoconch decollated; teleoconch of more than five whorls; suture overlapped by periphery of previous whorl. Surface of each whorl rather flat, sculptured by growth lines, axial ribs, and spiral cords; growth lines distinct and very oblique; axial ribs narrow, low, oblique in opposite direction to growth lines, 37 to 42 on penultimate whorl, 35 to 37 on last whorl, becoming more distinct near upper suture; spiral cords 6 to 13 on last
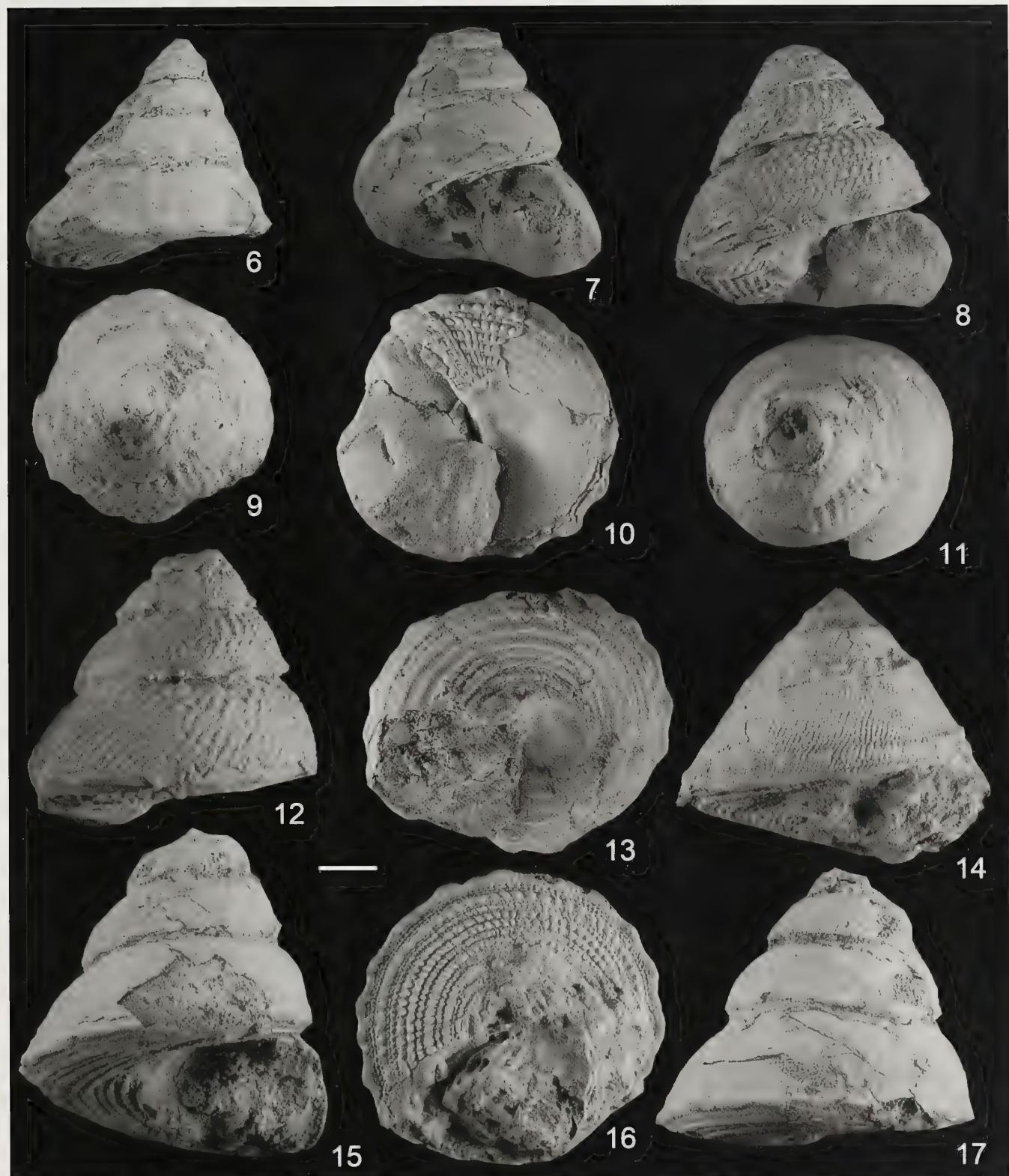
Figures 6–17. Fossil *Pomaulax* species from Japan. **6–13, 15, 17.** *Pamaulax omorii* (Shibata). **6, 9.** NMNS PM 28268. **6.** Abapertural view. **9.** Apical view; Tentokuji Formation. **7, 11.** NMNS PM 28270. **7.** Apertural view. **11.** Apical view; Araya Formation. **8, 10, 12.** NMNS PM 28271. **8.** Apertural view. **10.** Basal view. **12.** Abapertural view; Shitoka Formation. **13, 15, 17.** NMNS PM 28269. **13.** Basal view. **15.** Apertural view. **17.** Abapertural view. **14, 16.** *Pomaulax tyosiensis* (Ozaki), syntype NMNS PM 4257. **14.** Apertural view. **16.** Basal view; Na-Arai Formation. Scale bar = 10 mm.

whorl, forming granulations at intersection with axial ribs. Periphery with undulating carina bearing 14–15 nodes. Base flat, sculptured with five to nine spiral cords. Aperture oblique and squarely rounded in outline; umblical region covered by rather thick callus.

Remarks: The holotype specimen of *Pomaulax omorii* (Shibata, 1957) attains ca. 61 mm in height and 65mm in diameter. The topotype specimens illustrated by Matsushima et al. (2003) differ slightly from the holotype by their taller trochiform shape. Matsushima et al. (2003) also pointed out two forms having higher and lower spires.

Amano et al. (2000b) illustrated *Astralium* (*Distellifer*) aff. *rhodostoma* (Lamarck, 1822) from the upper Pliocene Tentokuji Formation at Kami-Sannai in Akita City, Akita Prefecture. However, from its size (max. 51.8 mm in shell height, 56.8 mm in diameter) and shell sculpture (37 to 42 axial ribs on the penultimate whorl, 14 to 15 nodes at the periphery, and five to nine sprial cords on the base), this species can be identified as *Pomaulax omorii*.

From the same locality as Amano et al. (2000b), Ogasawara et al. (1986) illustrated a poorly preserved specimen as *Omphalius pfeifferi* cf. *carpenteri* (Dunker, 1859). Judging from its size, shape and seven sprial cords on the base, this specimen probably can be identified with *Pomaulax omorii*.

Amano et al. (2011) illustrated two specimens as *Pomaulax omorii* from the lowermost Sasaoka Formation at the upstream of Ogurosawagawa River. However, one specimen in their fig. 5.14 has a noded spiral cord above the suture as in species of *Bolma* Risso, 1826.

Pomaulax omorii is closely allied to *P. tyosiensis* (Ozaki, 1954) from the Pliocene Na-arai Formation at Inuwaka in Choshi City, Chiba Prefecture. In the description of *P. tyosiensis*, Ozaki (1954) assigned Nat. Sci. Mus., coll. cat. no. 4257 as the holotype. However, as three specimens are included in the container under no. 4257, they should be considered as syntypes. I have examined all three specimens. *Pomaulax tyosiensis* (Figures 14, 16) differs from *P. omorii* in its two distinct rows of peripheral nodes like those of *Megastraea turbanica* (Dall, 1910), more fine and numerous axial ribs (132 on the last whorl), and more numerous peripheral nodes (13–16).

The Recent species *Pomaulax japonicus* (Dunker in Philippi, 1844) can be easily distinguished from *P. omorii* easily by having a larger and lower shell as well as no spiral cords on the last whorl.

Distribution: On the Pacific side of Honshu, upper Miocene Osozawa Sandstone Member of Iitomi Formation in Yamanashi Prefecture (Shiba et al., 2014) and lower Pliocene Ochiai Formation in Kanagawa Prefecture. On the Japan Sea side of Honshu, upper Pliocene Tentokuji Formation in Akita Prefecture, Araya and Shitoka formations in Niigata Prefecture.

DISCUSSION

Fossils of two species of *Monodonta* have been known from Japan: *M. minuta* Itoigawa and Nishikawa, 1976 and

M. labio (Linnaeus, 1758). The former species has been proposed from the lower Miocene Lower Member of the Bihoku Group in Okayama Prefecture (Itoigawa and Nishikawa, 1976). Nakagawa (2009) reported this species as *M. kanzakii* from the lower Miocene Kohnoura Shale Member of Shimo Formation in Fukui Prefecture. Later, Nakagawa (2018) synonymized *M. kanzakii* with *M. minuta*. The Recent species *M. labio* has been recorded from the middle Pleistocene Sakishima Formation in Mie Prefecture (Itoigawa and Ogawa, 1973), an upper Pleistocene deposit at Akaura in Ishikawa Prefecture (Matsuura, 1977), the Holocene Numa Coral Bed in Chiba Prefecture (Yokoyama, 1924), Holocene deposits at Hachigasaki and Onogi in Ishikawa Prefecture (Matsuura, 1985) and the Holocene Takahama shell bed in Fukui (Nakagawa et al., 1993). All these fossils are associated with warm-water faunas. In conclusion, *Monodonta joetsuensis* new species is the first record of *Monodonta* from the Pliocene in Japan. As mentioned above, two warm-water species are associated with *Monodonta joetsuensis* new species. The warm-water Tsushima current has flowed into the semi-enclosed Japan Sea for the past 4 Ma (Amano et al., 2008; Gallagher et al., 2015). Moreover, the temperature of this thin, in-flowing current in the late Pliocene was 3 to 4 °C higher than that of today (Amano et al., 2008; Amano, 2019). *Monodonta joetsuensis* new species related to *M. australis* possibly appeared along with the inflow of the warm-water current during the late Pliocene.

On the other hand, *Pomaulax omorii* appeared in the late Miocene to early Pliocene warm-water "Zushi-Ochiai type fauna" (Chinzei and Matsushima, 1987) or the "Zushi fauna" (Ozawa and Tomida, 1992) on the Pacific side of central Honshu. In the late Pliocene, this species invaded the Japan Sea to what is now the Akita Prefecture via the warm-water current. The occurrence of this species from the Araya and Shitoka formations seems to be nearly authochtonous. Judging from the habitat depth of living specimens of the associated recent species, the paleo-depth of both formations can be estimated as 100–200 m, which is slightly deeper than the Recent Japanese species, *Pomaulax japonicus* (0–100 m; Higo et al., 1999). This estimated paleodepth of *Pomaulax omorii* explains its co-occurrence with some bathyal mollucs from conglomerates of the Ochiai, Iitomi, and Tentokuji formations.

On the Atlantic side of North America and Europe, severe extinction of molluscan species resulted from the cooling event at the onset of major Northern Hemisphere Glaciation (NHG) around the end of the Pliocene (e.g. Stanley and Campbell, 1981; Stanley, 1986; Vermeij, 1991; Vermeij et al., 2008). The end-Pliocene extinction event was also recognized in corals and vertebrates (Woesik et al., 2012; Pimiento et al., 2017). When Sato and Kameo (1996) noticed the drastic change of nannofossils and increase of ice rafted debris (IRD) in the core from North Atlantic Ocean, they named this datum plane as Datum A (2.78 Ma, changed to 2.75 Ma by Sato et al., 2002) indicating the onset of glaciation and traced it in the land deposits in Akita Prefecture. Bailey et al. (2013) considered the onset of NHG at 2.72 Ma (MIS

Table 3. Molluscan species extinct by the end of the Pliocene in the Japan Sea borderland. $^{\circ}$temperate relict species from the Miocene; * warm-water species.

Species	Formation	Reference
Chlamys ingeniosa tanakai (Akiyama)$^{\circ}$	Arakurayama F., Ogikubo F.	Amano (1994)
C. insolita (Yokoyama)	Ogikubo F.	Amano (1994)
C. lioica shigaramiensis Amano and Karasawa	Ogikubo F.	Amano and Karasawa (1986)
Mizuhopecten yamasakii (Yokoyama)$^{\circ}$	Ogikubo F.	Amano (2001)
M. tryblium (Yokoyama)$^{\circ}$	Ogikubo F., Mita F.	Amano (2001), Amano et al. (2008)
M. naganoensis (Masuda)	Joshita F.	Amano and Sato (1995)
Neogenella hokkaidoensis (Nomura)$^{\circ}$	Joshita F.	Amano and Sato (1995)
Kaneharaia ausiensis (Ilyina)$^{\circ}$	Joshita F., Mita F., Nadachi F.	Amano and Sato (1995), Amano et al. (2008), this study
Protothaca tateiwai (Makiyama)$^{\circ}$	Joshita F., Tentokuji F., Mita F., Nadachi F.	Amano and Sato (1995), Amano et al. (2000b, 2008), this tudy
Humilaria perlaminosa (Conrad)	Kuwae F., Nadachi F.	Amano et al. (2000a), this study
Meretrix spp.	Takafu F. , Sarumaru F.	Nagamori and Yoshikawa (2019)
Thracia higashinodonoensis Oinomikado$^{\circ}$	Ogikubo F., Sasaoka F.	Amano (1995), Amano et al. (2011)
Pholadomya kawadai Omori$^{\circ}$	Tentokuji F.	Amano et al. (2011)
Monodonta joetsuensis new species*	Nadachi F.	this study
Pomaulax omorii (Shibata)*	Tentokuji F., Araya F., Shitoka F.	this study
Vermeijia japonica Amano	Sasaoka F., Kuwae F.	Amano (2019)
Glossaulax didyma coticazae (Makiyama)$^{\circ}$	Joshita F.	Amano and Sato (1995)
Ranella yasumurai Amano	Kuwae F.	Amano (1997)
Chicoreus totomiensis (Makiyama)*	Kuwae F.	Amano et al. (2000a)
Babylonia elata (Yokoyama)*	Mita F.	Amano et al. (2008)
Buccinum sinanoense Makiyama	Joshita F.	Amano and Watanabe (2001)
B. shibatense Amano and Watanabe	Kuwae F.	Amano and Watanabe (2001)
Cyllene satoi Amano*	Tentokuji F.	Amano (2019)
Scalptia kurodai (Makiyama)*	Tentokuji F.	Amano et al. (2000b)

G6), based on the abundant IRD deposition in the Nordic Seas and subpolar North Atlantic Ocean. Many cold-water species living now in Hokkaido migrated southward to central Honshu, and some Miocene-type relict mollusks suffered from extinction by the cooling event around 2.75Ma (Amano, 2001, 2007, 2019; Amano et al., 2011). Also, Pacific-type deep-water radiolarians disappeared from the Japan Sea around 2.75 Ma because of the intermittent development of low oxygen conditions in deep water (Itaki, 2016).

The grazers *Monodonta joetsuensis* new species and *Pomaulax omorii* also disappeared at the end of the Pliocene, probably as a result of the cooling event of the NHG. The species that probably became extinct at Datum A in the Japan Sea are shallow-water dwellers (Table 3). They include eight relict bivalves and the naticid *Neverita* (*Glossaurax*) *didyma coticazae* (Makiyama, 1926) which are temperate-water species that survived from the Miocene, and many warm-water gastropods. Also, it is interesting to note that the extinct species consist of suspension-feeding bivalves and grazing and predatory/scavenging gastropods. When Todd et al. (2002) examined the end-Pliocene extinction of mollusks in the Carribean region, they found that predatory gastropods and suspension feeding bivalves declined in abundance. This suggests that the nutrient supply changed by the cooling event of the NHG caused the faunal change even in the semi-enclosed Japan Sea.

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